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Fishery Bulletin

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Flow-related effects in prawn-trawl codends: potential for increasing the escape of unwanted fish through square-mesh panels

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Abstract.—Two experiments were done in a flume tank to quantify the effects of codend mesh circumference and weight of catch on water flow. The mesh circumference of the posterior section of prawn-trawl codends (with and without bycatch reducing square-mesh panels) were assessed with three weights of catch (30 kg, 50 kg, and 70 kg). Compared with a codend with a circumference of 100 meshes throughout its entire length, a codend with an anterior section of 100 meshes and a posterior section of 200 meshes in circumference significantly increased the displacement of water forwards (up to 1120 mm from the end of the codend). This result varied with the weight of catch in the codend. The second experiment involved placing composite panels of square-shaped mesh (bycatch reducing devices) into the tops of the anterior sections of two codends with the same configurations as those above (termed the "100 panel codend" and "200 panel codend," respectively). There was a displacement of water forwards immediately under the square-mesh panel in the 200 panel codend (by up to 2200 mm from the end of the codend). The results are discussed in terms of 1) the probable effects that codend mesh circumference and water displacement in codends have on fish behavior, and 2) implications for the future development of bycatch reducing devices like square-mesh panels in prawn-trawls.

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Oceanic prawn-trawling occurs from nine major ports in New South Wales (NSW) Australia and has a total value of approximately A$17 million per annum. The principal target species is the eastern king prawn (*Penaeus plebejus*), although a significant proportion of the total value is derived from the sale of legally retained bycatch comprising individuals of several species of fish, crustaceans, and cephalopods (see Kennelly, 1995). In addition to this landed catch, however, significant numbers of nontarget organisms of no commercial value are also captured and discarded, including juvenile fish of species which, when larger, are targeted in other commercial and recreational fisheries (Kennelly, 1995).

Concerns over the incidental capture and mortality of large numbers of juvenile fish have led to the development of various bycatch reducing devices (BRDs), designed to minimize undesirable bycatch while maintaining catches of prawns and other commercially valuable individuals (Broadhurst et al., 1996; Broadhurst and Kennelly, 1996; 1997). In particular, a new design comprising composite panels of square-shaped mesh (referred to as the composite square-mesh panel) was shown to increase catches of prawns (by up to 14%) (Broadhurst and Kennelly, 1997) while significantly reducing up to 40% of total unwanted bycatch and up to 70% of the numbers of small individuals of commercially important species such as whiting (*Sillago* spp.) (Broadhurst and Kennelly, 1996).

The results from these experiments are attributed primarily to differences in the behavior of fish and prawns in the trawl. Fish are believed to be herded close together in the anterior section of the codend, upsetting the normal balance of the school and initiating an escape response towards the sides and top of the net and out through the open square-shaped meshes (Broadhurst and Kennelly, 1996). A contributing factor towards this escape is the displacement and change in direction of water flow due to the circumfer-

ence of meshes in the posterior section of the codend. In an experiment to test this hypothesis, Broadhurst and Kennelly (1996) showed that a conventional codend made from an anterior section of 100 meshes circumference and a posterior section 200 meshes in circumference (a common commercial configuration) was less selective (i.e. retained more bycatch) than a conventional codend with a 100 mesh circumference throughout its entire length (see also Robertson and Stewart, 1988; Armstrong et al., 1990; Reeves et al., 1992; Galbraith et al., 1994). However, a comparison of codends with the same netting configurations as above but containing composite square-mesh panels located in their anterior sections showed that the effects on selectivity due to increased circumference in the posterior section were negated by a significant increase in the escape of small fish (e.g. red spot whiting, *Sillago flindersi*) through the square meshes.

These results led to the hypothesis that increased twine area and smaller mesh openings in codends with posterior sections of 200 meshes circumference increased the displacement of water forwards and out through the meshes in the anterior section (see also Watson, 1989). In turn, this water movement may have 1) physically directed small fish out through the strategically positioned composite square-mesh panel; 2) assisted them to maintain position in front of the catch in the codend, increasing their likelihood of randomly encountering square meshes; and (or) 3) stimulated their lateral line receptors and thus their overall escape response. The reaction of prawns to this stimuli was thought to be minimal, given their inability to sustain escape responses in trawls (see Lochhead, 1961; Newland and Chapman, 1989).

Although the results from the paper discussed above led to several hypotheses about changes in water flow and fish behavior due to changes in codend geometry, we lacked the quantitative information on flow rates necessary to support or refute them. Such information is important for developing new designs of codends and understanding where to position square-mesh panels and other BRDs. Our goals in the present study were to quantify the effects on water flow at various positions in codends and under square-mesh panels in two flume tank experiments. We simulated commercial conditions in the flume tank by using different weights of catch in various codend designs.

Materials and methods

Two experiments were undertaken in May 1996 at the Australian Maritime College with the Faculty of Fisheries and Marine Environment's flume tank. This facility consists of a recirculating flow tank of fresh water, measuring 17.2 m long, 5 m wide, and 2.5 m deep and comprises three levels: 1) an upper level where nets, etc., are placed into the tank; 2) an observation level, with a continuous perspex viewing-window; and 3) a water-return channel. The two lower levels feature a series of delivery bends and screens that maintain constant water velocity throughout the depth of the tank without any swirls or vortices. Several electric motors, hydraulic pumps, and impellor shafts provide water flow of up to 1.5 m/s.

An electromagnetic current meter was attached to the base of a stainless steel stanchion (Fig. 1A) and linked to a computer by means of a coaxial cable. The stanchion was attached to a movable carriage positioned on rails over the upper level of the flume tank. This assembly enabled the current meter to be repeatedly located at several predetermined positions within the tank.

A full-scale Florida flyer prawn-trawl (material: 18 ply twine; mesh size: 40 mm) with a headline length of 5.4 m, was rigged to two fixed stanchions, located on the sides of the forward section of the flume tank. The trawl was rigged with a zipper (no. 10 nylon open-ended auto-lock plastic slides) to facilitate changing the codends. The codends used in the experiments were of normal commercial size and materials, measuring 58 meshes long (2.3 m) and constructed from 40-mm mesh netting and 60-ply UV-stabilized high-density polyethylene twine. These codends comprised two sections: the anterior section, which was 33 meshes long and attached to a zipper and the posterior section, which was 25 meshes long (for details see Fig. 1, B and C —see also Broadhurst and Kennelly, 1996).

Experiment 1

Two codend designs were compared. The codends (termed the 100 and 200 commercial codends) were made entirely of diamond-shaped meshes and comprised anterior sections with a circumference of 100 meshes, attached to posterior sections with circumferences of 100 and 200 meshes, respectively (Fig. 1, B and C). Three incisions of the same size as the width of the current meter's stanchion (three meshes in length), were made in the tops of each codend at distances of 2200 mm, 1120 mm, and 560 mm forward from the end of the codends to facilitate placement of the current meter inside the codends (Fig. 1B).

Experiment 2

The two codends compared in this experiment were similar to the 100 and 200 commercial codends de-

scribed above but included composite square-mesh panels made of 60-mm and 40-mm netting (3-ply and 48-ply UV-stabilized high-density polyethylene twine, respectively) cut on the bar and inserted into the tops of the anterior sections (termed the 100 panel and 200 panel codends) (for details see Fig. 1C and Broadhurst and Kennelly, 1996). Because the current meter (and not its stanchion) was inserted only 5 cm into the tops of the codends (Fig. 1C), it was not necessary to cut the meshes of these codends. Instead, four positions were labeled with a permanent marker at 2200 mm, 1720 mm, 1490 mm, and 1130 mm forward from the end of the codends (Fig. 1C).

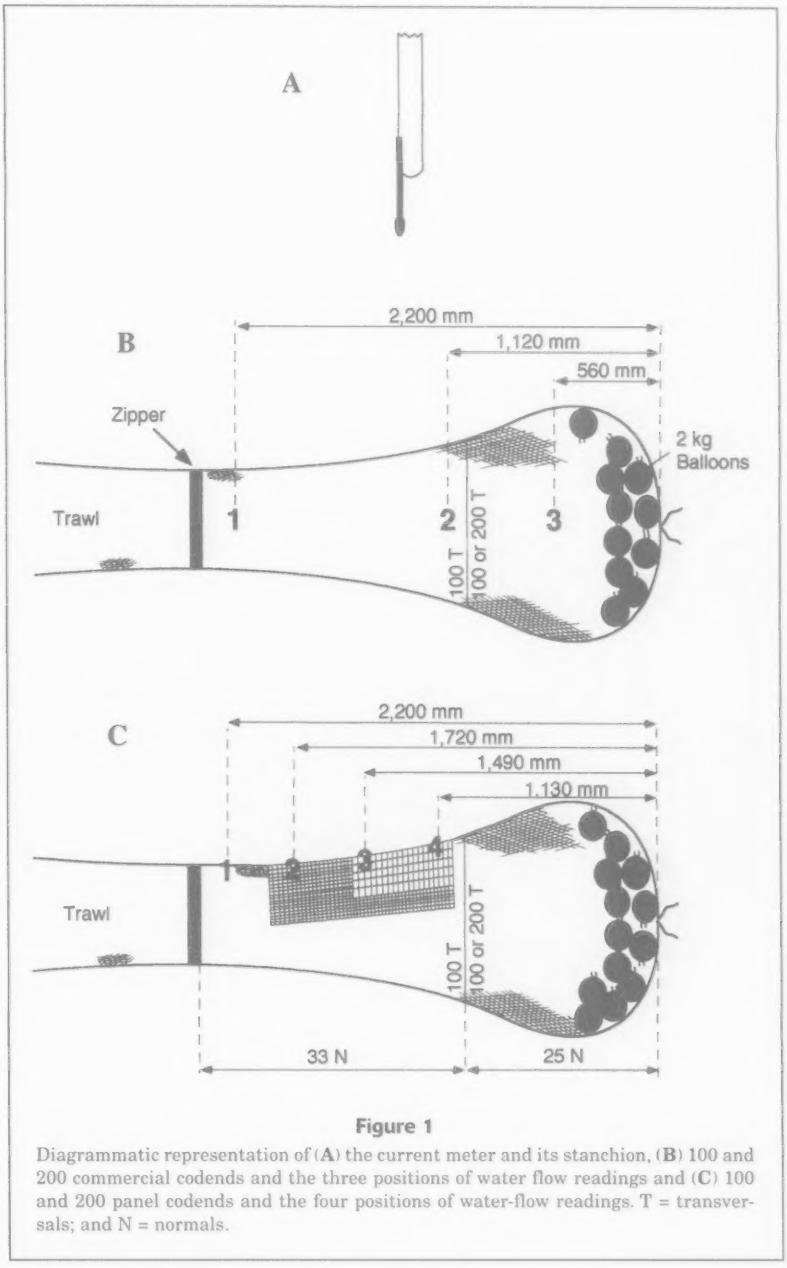

Figure 1

Diagrammatic representation of (**A**) the current meter and its stanchion, (**B**) 100 and 200 commercial codends and the three positions of water flow readings and (**C**) 100 and 200 panel codends and the four positions of water-flow readings. T = transversals; and N = normals.

Experimental procedure

Thirty five rubber balloons were each filled with 2 liters of water, providing a total mass (in air) of 70 kg. These balloons were used to simulate masses of catch in the codends. In each experiment, the two codends were tested alternately. The particular codend to be examined was attached to the trawl and loaded initially with 15 balloons (i.e. 30 kg). The hydraulic pumps in the flume tank were activated and adjusted to produce a flow of 1.2 m/s (the standard towing speed during commercial operations). After a stabilizing period of 10 minutes, the stanchion containing the current meter was alternately lowered into each of the predetermined positions in the codends (three in experiment 1 and four in experiment 2). After a further stabilizing period of one minute at each position, the current meter was switched on and left for a period of one minute, during which the flow of water immediately anterior to the current meter was recorded at one second intervals and the data were transmitted to the computer. The mean flow rate from each minute of recording was calculated from these data and used in subsequent analyses. After each reading, the current meter was moved to the next position and the procedure repeated. After six replicate readings were collected for each position, the flow of water in the flume tank was reduced to approx. 0.5 m/s and additional balloons were added to the trawl to simulate an increase

in the volume of catch. The above procedure was then repeated to obtain data on the flow of water at each position with 50 kg (25 balloons) and 70 kg (35 balloons) in each codend.

Data analysis

Data collected in each experiment were examined by using Cochran's test for homogeneity of variances and transformed if necessary. Data from experiment 1 were analyzed in a three-factor fully orthogonal, balanced analysis of variance. The factors were codends, positions, and weights. Data from experiment 2 were analyzed at each position in two-factor fully orthogonal, balanced analyses of variance (Underwood, 1981). Significant differences detected in these analyses were investigated by Student-Newman-Keuls (SNK) multiple comparisons of means.

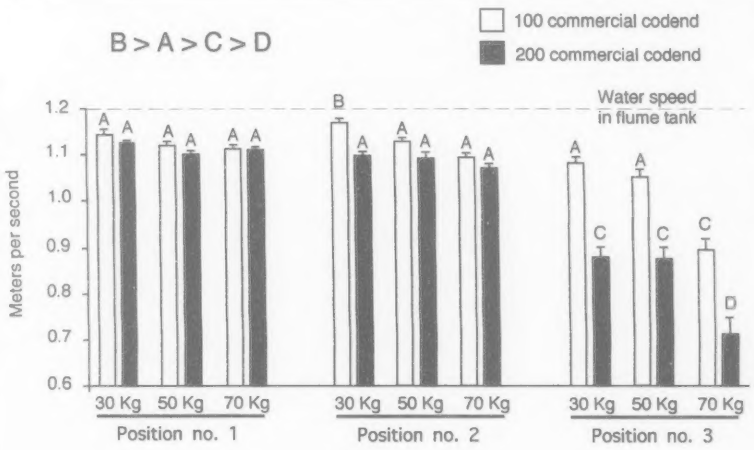

Figure 2

Differences in mean flow rates ±SE between the 100 and 200 commercial codends tested in experiment 1 (< and > indicate direction of differences in SNK tests).

Results

Experiment 1

The analysis of variance showed that there were significant differences in flow rates between the type of codend, position of the current meter and weight in the codend, and significant interactions among codend-type, positions and weights (Table 1). SNK tests showed that mean water flow was greatest at position no. 2 (1.162 m/s) in the 100 commercial codend with a catch of 30 kg and lowest at position no. 3 (0.709 m/s) in the 200 commercial codend with 70 kg (Fig. 2). SNK tests also showed that, compared with the 100 commercial codend, there was a significant reduction in mean water flow in the 200 commercial codend with 30 kg at position no. 2 (mean difference of 0.071 m/s) and across all three weights (30 kg, 50 kg, and 70 kg) at position no. 3 (mean differences of 0.203 m/s, 0.176 m/s and 0.184 m/s, respectively) (Fig. 2; Table 1). Although SNK tests did not detect differences in mean water flow between codends with 50 kg and 70 kg at position no. 2, nor across all weights at position no. 1, these combinations of weight and position showed trends similar to those described above—i.e. a mean reduction in water flow with the 200 commercial codend (Fig. 2).

Table 1

Summaries of F ratios from the analysis of variance to determine effects on water flow due to different codends (i.e. 100 and 200 commercial codends), position of current meter and weight in the codend. The square-root (sqrt(×)) transform was used to stabilize variances. In all tables $^{*}P = <0.05$; $^{**}P = <0.01$.

Treatment	df	Water flow (m/s)
Codends (C)	1	162.52**
Position (P)	2	388.16**
Weight (W)	2	62.42**
C × P	2	35.01**
C × W	2	8.04**
P × W	4	12.39**
C × P × W	4	0.81
Residual	90	

Experiment 2

There were significant differences in the mean water flow between the type of codend at position nos. 2, 3. and 4 and between weights at position nos. 2 and 3 (Table 2). There was a significant interaction between the type of codend and weight at position no. 1. SNK tests detected differences in the mean flow rates between the 100 and 200 panel codends at

Table 2

Summaries of F ratios from analyses of variance to determine effects on water flow at different positions due to different codends (i.e. 100 panel vs. 200 panel) and weights. The transforms used to stabilize variances (if required) are also listed.

Treatment	df	Position no. 1	Position no. 2	Position no. 3 sqrt(×)	Position no. 4
Codend (C)	1	2.21	5.88*	5.16*	7.92**
Weight (W)	2	2.29	3.95*	8.56**	1.34
C × W	2	7.81**	0.87	0.74	2.77
Residual	30				

position nos. 1, 3, and 4 (Fig. 3). Compared with the 100 panel codend, there was significantly less water flow in the 200 panel codend with a catch of 70 kg at position no. 1 (0.115 m/s difference between means) and at position no. 3 with 50 kg (difference of 0.102 m/s) (Fig. 3, A and C; Table 2). Conversely, at position no. 4, SNK tests detected an increase in the mean water flow in the 200 panel codend with a catch of 30 kg, compared with the 100 panel codend (difference of 0.067 m/s) (Fig. 3D). There was also a similar, although not significant result for 50 kg at this position. There were no other significant differences, although, at position nos. 2 and 3, there were similar trends across all weights (i.e. a reduction in water flow in the 200 panel codend) (Fig. 3, B and C).

Discussion

This study showed that the weight of catches and the configuration of the posterior section in codends can have significant effects on the displacement of water in the anterior section of codends. In interpreting these results, it is important to note that under the simulated conditions in the present study, water was forced through a stationary trawl (at 1.2 m/s). Any localized displacements of water forwards in the codends examined in this study, therefore, can be expressed as a reduction in the flow entering the trawl and calculated by subtraction from 1.2 m/s.

The flow of water at all positions in the four codends tested was less than 1.2 m/s, indicating that there was displacement of water anterior to the catch. However, the degree of this anterior water displacement varied significantly between the codends tested in each experiment (Figs. 2 and 3). For example, in experiment 1, the 200 commercial codend showed a significant increase (compared to the 100 commercial codend) in the displacement of water forwards at position no. 3 across all weights of catch (difference in mean flow of up to 0.203 m/s [Fig. 2; Table 1]). These differences in flow may be attributed primarily to the distribution of the balloons used to simulate catch in the two codends and consequent changes in codend geometry. In the 200 commercial codend, the balloons were observed to spread out evenly in the posterior section, providing a greater surface area of catch incidental to the flow than in the 100 commercial codend. This effect, combined with the increase in the area of twine in the 200 commercial codend probably caused an increase in the displacement of water forwards in this codend.

The above effects in the 200 commercial codend were also detected at position no. 2 with 30 kg of balloons and, although ANOVA failed to detect significant differences for the other weights at this position, the trends in the results were similar (i.e. a reduction in flow in the 200 commercial codend compared with the 100 commercial codend [Fig. 2; Table 1]). At position no. 1, for all weights, the force of the displaced water in front of the 200 commercial codend had dissipated to the extent where there were no significant differences between the two codends (Fig. 2; Table 1). It can be assumed, therefore, that the major influence of increased codend circumference on water displacement in the middle of the 200 commercial codend probably occurred up to some point between position nos. 2 and 3 (560 mm to 1120 mm from the end of the codend), in relation to the weight of catch.

In experiment 2, the effects of increased codend circumference on water displacement under the square-mesh panel were detectable at a greater distance from the end of the codend than those described above. Compared with the 100 panel codend, there were significant reductions in flow (corresponding to an increased displacement of water forwards) in the 200 panel codend at position nos. 1 and 3 (2200 mm and 1490 mm from end of the codend) with a weight of catch of 70 kg and 50 kg, respectively (mean differences in flow of 0.115 m/s and 0.102 m/s, respectively) (Fig. 3, A and C; Table 2). Although not significant, there were similar trends at position no. 2 for each weight and at position no. 3 for 30 kg and 70 kg (Fig. 3, B and C; Table 2). In contrast, there was a

significant increase in the flow of water at position no. 4 in the 200 panel codend with 30 kg and a similar result (though not statistically significant) for 50 kg (Fig. 3D; Table 2). This anomaly may be explained by the fact that the balloons in the 200 panel codend (like those in the 200 commercial codend) were orientated evenly across the surface area of the posterior section, increasing its diameter and decreasing the angle of incidence of its netting as it led into the anterior section of the codend at position no. 4. Although the current meter was located immediately under the composite square-mesh panel, at this position it was effectively aligned slightly above the anterior section of the codend and may have been influenced by the current outside the trawl, negating some of the flow-related effects of codend mesh circumference.

With the exception of this latter result, the measured reductions in flow at most positions in the 200 codends (corresponding to increases in water displacement forwards) support the hypothesis that an increase in the circumference of meshes in the codend contributes towards the escape of small fish (between 5 and 20 cm) through the composite square-mesh panel (see Broadhurst and Kennelly, 1996; 1997). The size of these fish suggests that they are using anaerobic muscle power to maintain position in the moving trawl (1.2 m/s) and are fatigued when they enter the codend (see Beamish, 1978; Wardle, 1989). A relatively small increase in the displacement of water forwards (e.g. 0.203 m/s at position no. 3 in the 200 commercial codend or 0.1 m/s at position no. 3 in the 200 panel codend) may be sufficient 1) to assist small fish to swim forwards and out through the square meshes in the panel and [or] 2) to enable them to reduce their tail-beat frequencies and maintain their position in the codend for a longer period, increasing their chances of random escape through the panel; and [or] 3) to stimulate their lateral line receptors and thus their overall escape.

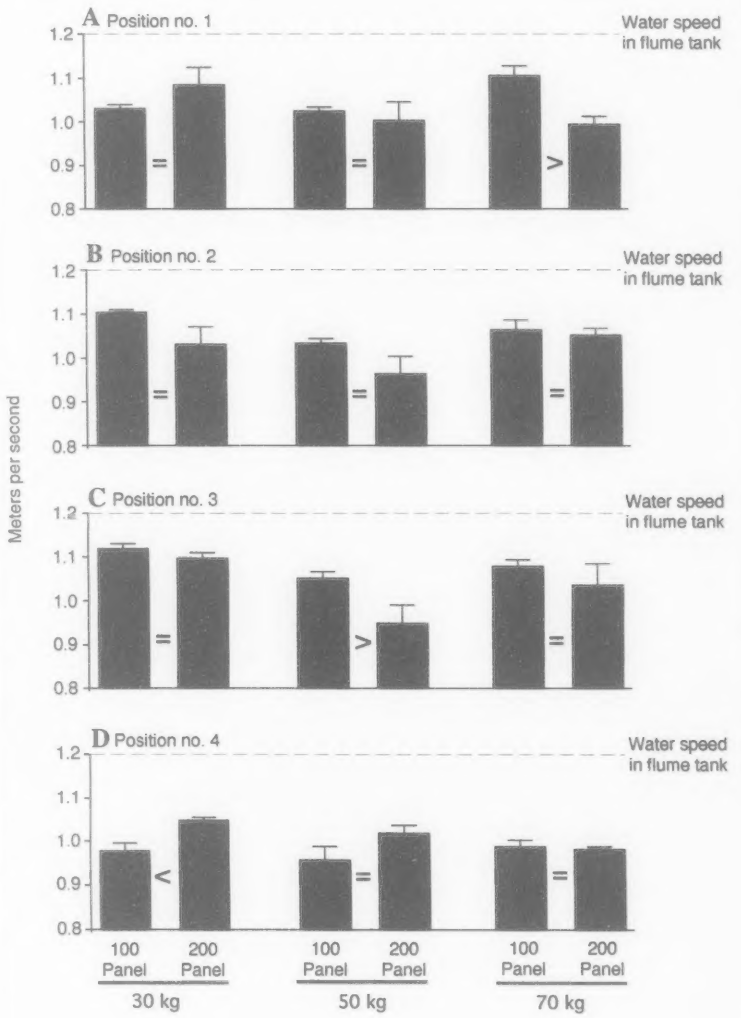

Figure 3

Differences in mean flow rates ±SE between the 100 and 200 panel codends tested in experiment 2 for each position of the current meter and for different weights (< and > indicate direction of differences in SNK tests of means).

Without direct observations of fish swimming in the codend, it is difficult to determine their specific behavior during escape. Whatever their actual escape mechanism, however, the results obtained in this study provide important information for the subsequent design and location of BRDs like the com-

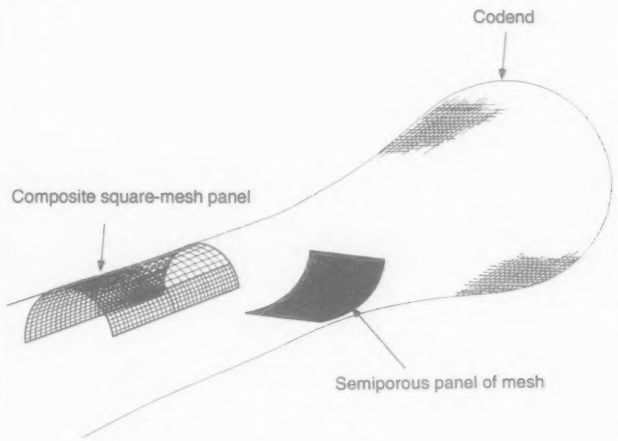

Figure 4

Diagrammatic representation of proposed modification to codends containing the composite square-mesh panel.

posite square-mesh panel. It is apparent that to maximize the effects of anteriorly displaced water in the posterior section of codends, the composite square-mesh panel should be located as close as possible to the end of the codend, but sufficiently in front of the anticipated build-up of catch to prevent prawns from accumulating past the square meshes and escaping through them. A solution to this problem would be to increase the codend mesh circumference in the posterior panel (i.e. the 200 panel codend), causing the catch to spread laterally in the back of the codend, rather than to accumulate in front. Although such a modification would also increase surface area, displacement of water forwards, and probably enhance fish escape through the square-mesh panel, it would also reduce mesh openings and the selectivity of the codend itself (Broadhurst and Kennelly, 1996).

An alternative modification that may increase displacement of water forwards (other than increasing codend circumference and catch) is to move the composite square-mesh panel forward in the codend and create areas of "artificial catch" by using semiporous panels (e.g. those with fine mesh). These could be positioned on the bottom of the codend, behind the panel and at an angle to the direction of tow (e.g. see Fig. 4). Such modifications would produce similar flow-related effects as those observed in our study, i.e. they would displace water anteriorly, directing fish towards the panel. Future research into the refinement of square-mesh panels and other BRDs in prawn-trawls that exploit the behavioral differences of fish in trawls, may benefit from these or similar modifications.

Acknowledgments

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An analysis of environmental effects on survey catches of squids *Loligo pealei* and *Illex illecebrosus* in the northwest Atlantic

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Abstract.—An analysis of environmental effects on autumn survey catches of two commercially exploited squid species, *Loligo pealei* and *Illex illecebrosus*, was conducted. Research survey data collected during 1967–94 were used to determine the significance and relative importance of average depth of tow, time of day, bottom temperature, and surface temperature on bottom trawl catches of *L. pealei*, a neritic species, and *I. illecebrosus*, an oceanic species. We examined habitat associations of both species by using randomization methods and found that *L. pealei* was consistently associated with all of the environmental factors examined. In comparison with *L. pealei*, catches of *I. illecebrosus* were much lower and associations with environmental factors were inconsistent. We also examined whether environmental conditions affected catches of juvenile and adult squid differentially. Depth had an important effect on the magnitude of juvenile and adult *L. pealei* catches, with the ratio of juvenile to adult catches decreasing with depth. Depth had a similar, but less pronounced, effect on *I. illecebrosus* catches. Time of day also affected *L. pealei* and *I. illecebrosus* catches. Catches of both species were lowest at night and diel effects were more pronounced for juveniles than for adults. Bottom and surface temperatures had a substantial effect on catches of juvenile and adult *L. pealei* but had a variable influence on *I. illecebrosus* catches. The joint effects of depth stratification, time of day, and annual squid abundance on survey catches were also analyzed to determine correction factors for diel differences in catchability of juvenile and adult squid. Significant diel differences in catchability were detected for juvenile and adult *L. pealei* and for juvenile *I. illecebrosus* and diel correction factors were determined for survey catches of these size categories. In contrast, significant diel differences in catchability of adult *I. illecebrosus* were not detected.

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An analysis of environmental effects on survey catches of two commercially exploited squid species, *Loligo pealei* and *Illex illecebrosus*, was conducted for the continental shelf of the United States in the northwest Atlantic. Research survey data, collected during autumn, were used to determine the significance and relative importance of average depth of tow, time of day, bottom temperature, and surface temperature on bottom trawl catches of *L. pealei*, a neritic species, and *I. illecebrosus*, an oceanic species. Both squids grow rapidly (Brodziak and Macy, 1996; Dawe and Beck[1]), appear to live less than one year (Hurley et al., 1985; Macy, 1995; Brodziak and Macy, 1996; Dawe and Beck[1]), and undertake seasonal migrations in response to fluctuations in food availability, water temperature, and spawning (Lange and Sissenwine, 1983; Rowell et al., 1985a; O'Dor and Coelho, 1993). The rapid growth and short lifespan of these sympatric species suggest that environmental conditions were probably important determinants of their distribution and abundance on the continental shelf.

We investigated whether there was empirical evidence of habitat associations for both species by applying the habitat association method of Perry and Smith (1994). This randomization method accounted for the stratified random sampling design of the Northeast Fisheries Science Center (NEFSC) survey and tested whether catches within a year were associated with depth, time of day, surface temperature, and bottom temperature. Within-year associations that were consistent through time indicated which environmental conditions affected distribution and also provided a qualitative indication of habitat preferences.

We also examined whether environmental conditions affected catches of juvenile and adult squid differentially. Juveniles and adults of both species tend to differ in their food habits (Vovk, 1972; Vinogradov and Noskov, 1979; Macy, 1982; Maurer and Bowman, 1985) and, as a result, may use different habitats for feeding. We compared the effects of average depth of tow, time of day,

[1] Dawe, E. G., and P. C. Beck. 1992. Population structure, growth, and sexual maturation of short-finned squid at Newfoundland, Canada, based on statolith analysis. ICES Council Meeting, Shellfish Committee/K, 33 p.

and surface and bottom temperature on survey catches to determine whether the habitat preferences of juveniles and adults overlap. Potential effects of different categories of depth, time of day, and surface temperature and bottom temperature on mean catch per tow were tested for juveniles and adults of both species, and the potential impacts on the ratio of juvenile to adult catches were also examined. These analyses also suggested whether environmental effects were similar for these sympatric species, because the degree of spatial overlap between their geographic distributions is at a maximum during autumn.

Last, we evaluated the relative magnitude of diel effects on juvenile and adult squid catches in relation to survey design and fluctuations in annual squid abundance. Previous bottom trawl studies have shown that diel effects on catches of *L. pealei* and *I. illecebrosus* can be important (Roper and Young, 1975; Sissenwine and Bowman, 1978; Lange and Sissenwine, 1983; Arkhipkin and Fedulov, 1986; Shepherd and Forrester[2]) because greater catchability occurs during the day. As a result of diel vertical migrations, night catches of these two species can be biased low in relation to day catches. To account for diel effects on minimum swept-area estimates of *L. pealei* biomass and stock size, diel correction factors have been used to adjust nighttime bottom trawl catches to daytime equivalents (Lange and Sissenwine, 1980, 1983). However, these correction factors were developed for total numbers of squid and were not size specific, even though Sissenwine and Bowman (1978) noted that a sixfold difference between the diel correction factor for weight and numbers of *L. pealei* suggested differential vertical migration by size. In this study, we applied a general linear model to determine size-specific diel correction factors for *L. pealei* and *I. illecebrosus* that accounted for potential effects of survey design and fluctuations in annual abundance. When diel effects were significant, correction factors were determined to standardize nighttime catches to daytime units.

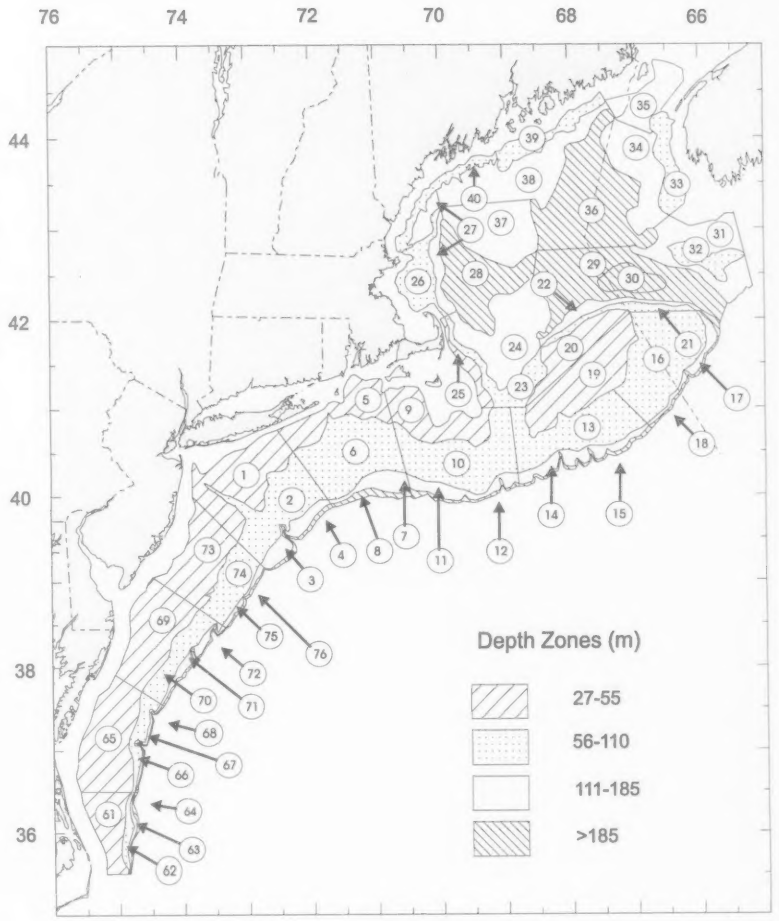

Figure 1

Offshore depth strata for autumn Northeast Fisheries Science Center bottom trawl surveys, 1963–94.

Materials and methods

Survey data

Research survey data were analyzed from NEFSC autumn bottom trawl surveys conducted during 1967–94 between Cape Hatteras, North Carolina, and the Gulf of Maine. In general, autumn surveys were conducted from mid-September through mid-

[2] Shepherd, G., and J. Forrester. 1987. Diurnal variation in catchability during bottom trawl surveys off the Northeastern United States. ICES Council Meeting 1987/B:44 (mimeo), 15 p.

October and along a similar cruise track each year. Standardized survey gear, procedures, and the stratified random sampling design are described in Azarovitz (1981). Offshore survey strata are defined by four depth zones; ranging between 27 m and 366 m. Strata numbers 1–30, 33–40, and 61–76 were included in our analyses (Fig. 1). Sampling was conducted 24 hours a day. Autumn survey data were used because only in autumn are both squid species distributed primarily within the survey sampling area. Survey data during 1963–66 could not be analyzed because catches of squid were not separated by species during these years.

At each randomly selected survey station, sampling was performed with a no. 36 Yankee otter trawl rigged with roller gear. Only standard tows, consisting of 20–30 minutes duration at a vessel speed of 3.5 knots, were included in the analyses. After each tow, the total weight of *L. pealei* and *I. illecebrosus* was measured to the nearest 0.1 kg, each species was enumerated, and length-frequency data (mantle length [ML] measured to the nearest cm) were collected. The following hydrographic and navigational data were recorded for each station: depth at the start and end of every tow (m), time of tow (h:m, Eastern Standard Time), bottom water temperature (°C), and surface water temperature (°C). Towing depth was computed as the average of depths recorded at the start and end of each tow. Surface water temperature was included in this analysis because the effect of surface temperature on the vertical distribution and catchability of these squids was unknown but was anecdotally important and potentially different from the effect of bottom temperature during autumn. In general, bottom and surface water temperatures within the survey region vary during autumn owing to the transition from a stratified water column, characteristic of summer, to a well-mixed condition typical of winter (Bowman, 1977). In particular, the relationship between surface and bottom water temperatures varied on an annual basis during the 1967–94 autumn surveys. Surface and bottom temperatures were not significantly correlated in 8 out of 28 years (29%), and exhibited a positive correlation ($\bar{\rho}$ =0.43) in 19 out of 28 years (68%) during 1967–94.

When an environmental factor was not measured at a survey station, that station was excluded from the association test for that factor. Stations with missing environmental measurements occurred at random, with the exception of the Georges Bank portion of the autumn 1990 survey when no bottom temperature measurements were made. In total, 7177, 7179, 6105, and 6280 stations were available for the association tests of squid catch with depth, time of day, bottom temperature, and surface temperature, respectively.

Within-year associations

Perry and Smith (1994) developed a nonparametric test of association between an environmental factor and the quantity of catch during a stratified random survey. Their method uses the maximum absolute difference between the cumulative distribution function (CDF) of an environmental factor and the catch-weighted CDF of that environmental factor as a test statistic in a randomization procedure to evaluate whether a significant association exists. In particular, the test algorithm is as follows. First, the empirical CDF (f) of the environmental factor is computed as

$$f(t) = \sum_h \sum_i \frac{W_h}{n_h} I(x_{ih}), \tag{1}$$

where t = the value of the environmental factor;
h = an index for the survey strata;
i = an index for the tow in stratum h;
x_{ih} = the observed value of the environmental factor from the i^{th} tow in stratum h;
W_h = the proportion of the survey area in stratum h;
n_h = the number of tows in stratum h; and
$I(x)$= an indicator function with $I(x)$=1, when $x \le t$, and $I(x)$=0, when $x > t$.

Second, the empirical cumulative distribution of catch as a function of the environmental factor (g) is computed as

$$g(t) = \sum_h \sum_i \frac{W_h y_{ih}}{n_h \bar{y}_{st}} I(x_{ih}), \tag{2}$$

where $$\bar{y}_{st} = \sum_h W_h \bar{y}_h,$$

and where y_{ih}= the catch from the i^{th} tow in stratum h;
$\bar{y}_h$ = the mean catch in stratum h; and
$\bar{y}_{st}$ = the stratified mean catch.

In Equation 2 above, the quotient $y_{ih}/\bar{y}_{st}$ expresses the relative catch under environmental condition x_{ih} in comparison with the stratified mean. The maximum absolute value of the difference between $f(t)$ and $g(t)$ over all values of the environmental factor is the observed test statistic (T) where

$$T = \underset{\forall t}{MAX} \left| \sum_h \sum_i \frac{W_h}{n_h} \left(\frac{y_{ih} - \bar{y}_{st}}{\bar{y}_{st}} \right) I(x_{ih}) \right|. \tag{3}$$

To evaluate whether the test statistic is significant, the observed environmental measurements (x_{ih}) are randomly sampled with replacement and assigned to observed catches with probability W_h/n_h under the hypothesis that the association between catch and the environmental factor is random. The value of the test statistic (T_R) is then computed for this random assignment. The randomization procedure of assigning environmental measurements to catches and of computing the value of T_R is repeated a large number of times to generate a distribution of test statistics for the null hypothesis of random association between catch and environmental factor. Last, the observed test statistic T is compared to the distribution of test statistics T_R from the randomization procedure to evaluate whether the null hypothesis of random association can be rejected.

We applied this test to *L. pealei* and *I. illecebrosus* catch, in numbers per tow, using four environmental factors: average depth of tow, time of tow, bottom water temperature, and surface water temperature. A total of 2000 randomizations were performed to provide an empirical distribution based on 2001 test statistics, including the original test statistic.

Size-specific environmental effects

Size-specific environmental effects on mean catches were evaluated separately for each species using tows that captured both juveniles and adults to ensure that comparisons were made under the same environmental conditions and that the ratio of juvenile to adult catch was well defined. Catch numbers of squid were separated into prerecruit (≤8 cm ML for *L. pealei* and ≤10 cm ML for *I. illecebrosus*) and recruit (>8 cm ML for *L. pealei* and >10 cm ML for *I. illecebrosus*) size categories, where prerecruits and recruits roughly corresponded to juvenile and adult squid. In what follows, prerecruit and recruit categories will sometimes be colloquially referred to as juveniles and adults, respectively. However, both *L. pealei* (Macy, 1980) and *I. illecebrosus* (Coelho and O'Dor, 1993) exhibit variability in sex-specific size at maturity, and for both species, an unmeasured fraction of smaller individuals within the recruit category were juveniles. The effect of depth on mean catch was evaluated first. Tow depth was categorized according to the depth zones used to define offshore strata of the NEFSC bottom trawl surveys: depth zone I (27–55 m), zone II (56–110 m), zone III (111–185 m), and zone IV (186–366 m). Similarly, time of tow was categorized into three time zones: zone I (night: 20:00–23:59 and 00:00 to 3:59), zone II (dawn and dusk: 4:00–7:59 and 16:00–19:59), and zone III (day: 8:00–15:59). Bottom and surface temperatures were grouped into three zones based on the 25th (P_{25}) and 75th (P_{75}) percentiles of the empirical temperature distribution of each of these two variables. Temperature zone I was P_0 to P_{25}, zone II was P_{25} to P_{75}, and zone III was P_{75} to P_{100}. Mean catches between zones were compared after applying a logarithmic transformation to stabilize the variance of number per tow. Similarly, mean ratios of juvenile to adult catches were compared between zones after applying a logarithmic transformation to the ratio. Mean $\log_{10}$-transformed catch per tow values of juveniles and adults and their ratios were tested at the 5% level of significance by using the GT-2 test which is appropriate for unplanned comparisons with unequal sample sizes (Sokal and Rohlf, 1981). Only the effects of individual environmental factors on juvenile and adult catches were evaluated in these univariate tests and the potentially important factors of interannual changes in abundance or of survey stratification were subsumed into random variation.

Diel correction factors

We analyzed the combined effects of survey design, time of day, and annual squid abundance to determine correction factors for diel differences in catchability of juvenile and adult squid. As in the evaluation of size-specific environmental effects, catches (C) from tows that captured both juveniles and adults were $\log_{10}$-transformed. A general linear model (Searle, 1987) was applied to estimate the effects of survey stratum (Fig. 1), time of day category, and year on $\log_{10}$-transformed catches. Time of day was categorized into three time zones: zone I (night: 20:00–23:59 and 00:00–3:59), zone II (dawn and dusk: 4:00–7:59 and 16:00–19:59), and zone III (day: 8:00–15:59) so that the time period effect (T) measured diel differences in mean catch. The year effect (Y) provided a measure of the effect of changes in relative annual abundance on mean catch whereas the survey stratum effect (S) accounted for the effects of geographic location and depth. The general linear model (GLM) was

$$\log C_{ijk} = \log U_R + \log T_i + \log Y_j + \log S_k + \varepsilon_{ijk}, \quad (4)$$

where C_{ijk} = mean catch during the i^{th} time period (T_i) in the j^{th} year (Y_j) within the k^{th} stratum (S_k);

U_R = mean catch in a standard reference cell (where standard time period=day, year=1994, and survey stratum=1); and

ε_{ijk} = an independent and identically distributed normal random variable with zero mean and constant variance σ^2.

Parameters of the GLM model were estimated using ANOVA for both prerecruit and recruit catches of each species. The significance of time, year, and stratum effects were evaluated by using type-III sums of squares that do not depend on the order in which effects are added to the model (Searle, 1987). Because daytime was the reference time period, the diel coefficient for the daytime had the value 1. Point estimates and confidence intervals of time zone I (T_I) and II (T_{II}) coefficients in relation to the daytime coefficient were computed whenever the diel effect was significant. Given estimates of T_I and T_{II}, catches (y_{ih}) made during time zone I or II period can be corrected to daytime catch units by dividing them by the diel effects coefficient as y_{ih}/T_I and y_{ih}/T_{II}, respectively. Diel-standardized, stratified mean catches ($\bar{y}_{st}^*$) can be expanded by the total number of sampling units within the survey region (N) to provide minimum swept-area estimates of juvenile or adult population size ($N\bar{y}_{st}^*$) and variance ($N^2\ Var[\bar{y}_{st}^*]$) within the survey region using stratified random sampling estimators (Cochran, 1977).

Results

Within-year associations

The neritic squid species exhibited different degrees of within-year habitat associations than those exhibited by the oceanic species. Results of the randomization tests of *L. pealei* catches with depth, time of day, bottom temperature, and surface temperature (Table 1) showed that *L. pealei* catch was consistently associated with each of these factors. Associations were significant ($P<0.05$) in all years for depth, bottom temperature, and surface temperature. For time of day, associations were significant in all years except 1980 (96%). In contrast, results of the randomization tests for *I. illecebrosus* (Table 2) indicated that catches of this species were inconsistently associated with only some of the factors. During the 28 years analyzed, a total of 15, 13, 7, and 12 associations were significant for depth, time of day, bottom temperature, and surface temperature, respectively. All four factors were significantly associated with *I. illecebrosus* catch during 1983; otherwise, there was no apparent pattern of annual associations. Overall, *L. pealei* exhibited consistent within-year associations, whereas *I. illecebrosus* exhibited variable within-year associations with the four environmental factors.

We compared the interquartile range of the catch-weighted CDF of each factor to the interquartile range of its unweighted CDF to see how associations varied across years. For brevity, the term "midrange" denotes the "average interquartile range" in what follows. For depth, this comparison of CDFs showed whether *L. pealei* or *I. illecebrosus* preferred shallower or deeper water in relation to observed depths. The midranges of depth for *L. pealei* and *I. illecebrosus* catches were 37–75 m and 79–149 m (Fig. 2A), respectively, whereas the midrange of all observed depths was 51–166 m. For *L. pealei*, the average of the median catch-weighted depth was 50 m, about 35 m shallower than the average observed depth and equal to the P_{25} of the observed depths. In contrast, the average of the median catch-weighted

Table 1

Results of univariate randomization test of association between catches of *L. pealei* and depth, time of day, bottom temperature, and surface temperature, during the NEFSC autumn bottom trawl survey, 1967–94. Table entries are the probabilities of random association[1] between *L. pealei* catches and the environmental factor. The symbol "*" denotes probability values of $0.05 \geq P > 0.01$, and the symbol "**" denotes the probability values of $0.01 \geq P$.

	Environmental factor			
Year	Average depth	Time of day	Bottom temperature	Surface temperature
1967	0.00**	0.00**	0.00**	0.00**
1968	0.00**	0.00**	0.00**	0.00**
1969	0.00**	0.00**	0.00**	0.00**
1970	0.00**	0.00**	0.00**	0.00**
1971	0.03*	0.00**	0.00**	0.00**
1972	0.00**	0.00**	0.00**	0.00**
1973	0.04*	0.00**	0.00**	0.00**
1974	0.00**	0.00**	0.00**	0.00**
1975	0.00**	0.00**	0.00**	0.00**
1976	0.00**	0.00**	0.00**	0.00**
1977	0.00**	0.00**	0.00**	0.00**
1978	0.00**	0.00**	0.00**	0.00**
1979	0.00**	0.00**	0.00**	0.00**
1980	0.00**	0.07	0.00**	0.00**
1981	0.00**	0.00**	0.00**	0.00**
1982	0.01**	0.00**	0.03*	0.00**
1983	0.01**	0.00**	0.00**	0.00**
1984	0.00**	0.00**	0.00**	0.00**
1985	0.00**	0.00**	0.00**	0.00**
1986	0.01**	0.00**	0.00**	0.00**
1987	0.00**	0.00**	0.00**	0.00**
1988	0.00**	0.02*	0.00**	0.00**
1989	0.00**	0.00**	0.02*	0.00**
1990[1]	0.00**	0.00**	0.00**	0.00**
1991	0.00**	0.00**	0.00**	0.00**
1992	0.00**	0.00**	0.00**	0.00**
1993	0.02*	0.01**	0.00**	0.00**
1994	0.00**	0.00**	0.00**	0.00**

[1] No bottom temperature data were collected on Georges Bank during 1990.

depth for *I. illecebrosus* was 106 m, roughly 20 m deeper than the average observed depth. Overall, *L. pealei* was consistently associated with shallow depths (37–75 m), whereas *I. illecebrosus* was more common in deeper waters (79–149 m).

The comparison of midranges for time of day indicated whether *L. pealei* or *I. illecebrosus* catches were more prevalent during night or day. We measured time in relation to a reference time of day (6:00 AM EST) because this roughly corresponds to first light, during autumn, when diel effects on the behavior of squid might be expected to change. This choice did not affect the results of the habitat association test; however, median time of day was 18:00 EST, instead of 12:00 noon EST. The midranges for time of day for *L. pealei* and *I. illecebrosus* catches were 10:00–17:00 EST and 10:00–18:00 EST, respectively (Fig. 2B). In comparison, the midrange for time of day was 13:00–1:00 EST. For both *L. pealei* and *I. illecebrosus*, the average median catch-weighted time of day was 14:00 EST, roughly 4 hours earlier than the average median time of 18:00 EST, and roughly equal to P_{25} of the overall time distribution. Overall, both *L. pealei* and *I. illecebrosus* exhibited diel catchability because squid catches were consistently greater during day than at night.

Table 2

Results of univariate randomization test of association between catches of *I. illecebrosus* and depth, time of day, bottom temperature, surface temperature during the NEFSC autumn bottom trawl survey, 1967–94. Table entries are the probabilities of random association[1] between *I. illecebrosus* catches and the environmental factor. The symbol "*" denotes probability values of $0.05 \geq P > 0.01$, and the symbol "**" denotes the probability values of $0.01 \geq P$.

	Environmental factor			
Year	Average depth	Time of day	Bottom temperature	Surface temperature
1967	0.13	0.01**	0.01**	0.00**
1968	0.03*	0.24	0.05*	0.01**
1969	0.08	0.03*	0.26	0.33
1970	0.16	0.15	0.02*	0.02*
1971	0.01**	0.01**	0.00**	0.08
1972	0.24	0.30	0.12	0.03*
1973	0.04*	0.13	0.71	0.12
1974	0.52	0.03*	0.03*	0.23
1975	0.34	0.00**	0.77	0.00**
1976	0.02*	0.20	0.54	0.30
1977	0.04*	0.44	0.26	0.01**
1978	0.12	0.00**	0.87	0.03*
1979	0.00**	0.15	0.07	0.07
1980	0.01**	0.01**	0.24	0.25
1981	0.61	0.01**	0.51	0.25
1982	0.03*	0.00**	0.09	0.18
1983	0.03*	0.00**	0.01**	0.00**
1984	0.03*	0.47	0.42	0.00**
1985	0.00**	0.00**	0.24	0.12
1986	0.03*	0.51	0.60	0.31
1987	0.39	0.34	0.53	0.04*
1988	0.98	0.12	0.06	0.34
1989	0.69	0.10	0.32	0.58
1990[1]	0.00**	0.00**	0.27	0.09
1991	0.04*	0.36	0.11	0.48
1992	0.13	0.01**	0.00**	0.00**
1993	0.33	0.24	0.53	0.03*
1994	0.04*	0.18	0.09	0.39

[1] No bottom temperature data were collected on Georges Bank during 1990.

Potential effects of bottom temperature were also examined to see whether *L. pealei* or *I. illecebrosus* preferred warmer or cooler bottom temperatures. The midranges of bottom temperature for *L. pealei* and *I. illecebrosus* catches were 11–15°C and 9–13°C, respectively, and the midrange for bottom temperature was 8–13°C (Fig. 2C). For *L. pealei*, the average of the median catch-weighted bottom temperature was 13°C, about 3°C warmer than the average of the overall bottom temperature distribution. For *I. illecebrosus*, the average of the median catch-weighted bottom temperature was 11°C, which was nearly equal to the average of the observed bottom temperature distribution Although *L. pealei* was associated with warmer bottom temperatures, it did not appear that *I. illecebrosus* was closely associated with bottom temperature.

Effects of surface temperature were also examined to see whether *L. pealei* or *I. illecebrosus* preferred warmer or cooler surface temperatures. The midranges of surface temperature for *L. pealei* and *I. illecebrosus* catches were 17–20°C and 13–20°C (Fig. 2D), respectively, and the midrange for all surface temperatures was 11–19°C. For *L. pealei*, the average of the median catch-weighted surface temperature was 18°C; about 4°C warmer than the average overall surface temperature distribution. Similarly, the median catch-weighted surface temperature of 16°C for *I. illecebrosus* was 2°C warmer than this average. Overall, *L. pealei* was generally associated with warmer surface temperatures, whereas *I. illecebrosus* associations were more variable, and this species was less frequently associated with warmer surface temperatures.

Size-specific environmental effects

Mean catches of *L. pealei* prerecruits and recruits varied across depth zones (Fig. 3A) where combined sample sizes for depth zones I, II, III, and IV were 1234, 1012, 270, and 99 tows, respectively. Mean catches of prerecruits peaked in zone I and declined

with depth, whereas mean catches of recruits peaked in zone III. The lowest mean catch of *L. pealei* prerecruits and recruits occurred in the deepest strata, zone IV. There was no significant difference between mean catches of prerecruits in depth zones II and III or recruits in zones I and II or zones II and III (Fig. 3A). The mean ratio of prerecruit to recruit catches was highest in depth zone I (Fig. 3B) and exhibited a declining trend with depth. However, the mean ratio was not significantly different in depth zones II, III, and IV. Overall, catches of *L. pealei* prerecruits decreased with depth, whereas recruit catches peaked at intermediate depths (111–185 m).

For *I. illecebrosus*, mean catches exhibited heterogeneity across depth zones (Fig, 3C), where sample sizes for depth zones I, II, III, and IV were 85, 283, 161, and 81 tows, respectively. Mean catches of recruits increased with depth and were highest in depth zone IV, whereas mean catches of prerecruits were relatively homogeneous across depths but were lowest in zone II. For prerecruits, mean catches were significantly different only between zones I and II (Fig. 3C). In contrast, mean catches of recruits were significantly different between all depth zones except zones III and IV and zones II and III. The mean ratio of prerecruit to recruit catches peaked in zone I, whereas the mean ratios in zones II, III, and IV were not significantly different (Fig. 3B). Overall, catches of *I. illecebrosus* prerecruits peaked in the shallowest depth zone (27–55 m) but were similar at greater depths. Similar to those of *L. pealei*, catches of *I. illecebrosus* recruits increased with depth as the ratio of prerecruit to recruit catch decreased with depth.

As expected, mean catch of *L. pealei* prerecruits and recruits peaked during day and were lowest at night (Fig. 4A). Sample sizes for time zones I, II, and III were 518, 968, and 1129 tows, respectively. For prerecruits, mean catch by time of day differed significantly for all three time zones (Fig. 4A), whereas mean catches of recruits were not significantly different between those for time zone II and zone III. The mean ratio of prerecruit to recruit catches peaked during day and was lowest at night (Fig. 4B), whereas the mean ratios for all time zones were significantly different (Fig. 4B). Overall, catches of both *L. pealei* prerecruits and recruits increased during day, although the difference between day and night catches was more pronounced for prerecruits.

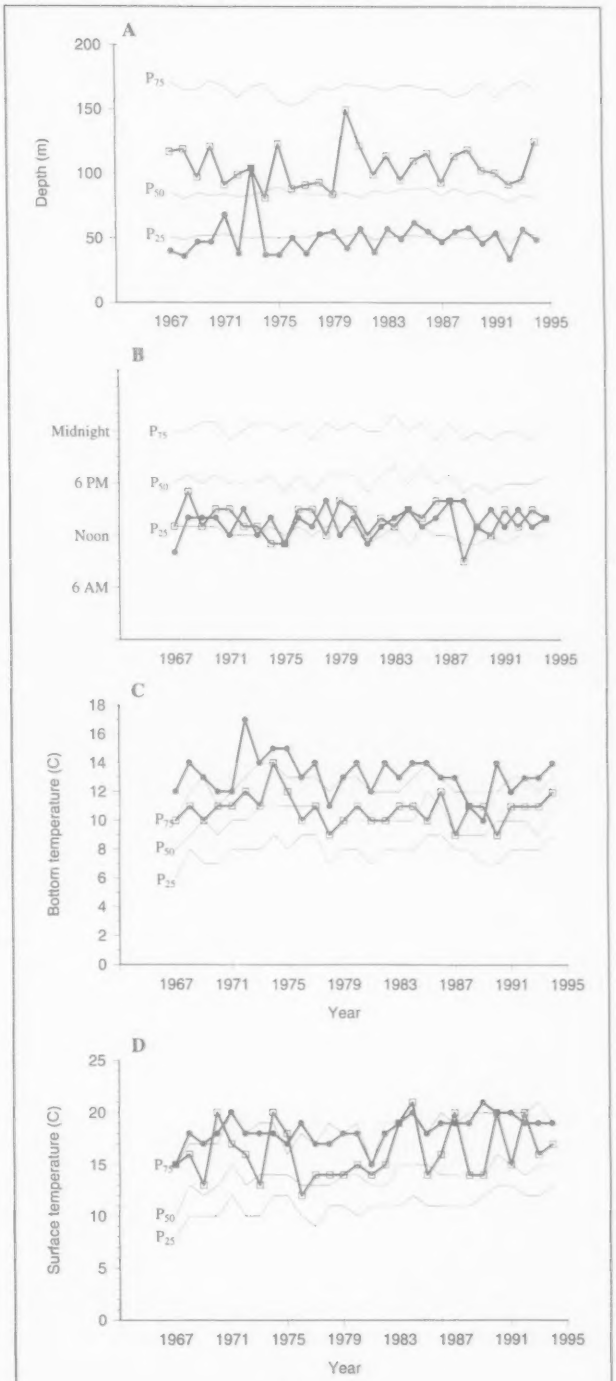

Figure 2

Catch-weighted averages of (**A**) depth (m), (**B**) time of day (h), (**C**) bottom temperature (°C), and (**D**) surface temperature (°C) by year for *L. pealei* (solid circle) and *I. illecebrosus* (open square). The 25th, 50th, and 75th percentiles (P_{25}, P_{50}, and P_{75}, thin solid lines) of the annual autumn distribution of each environmental factor are provided for comparison.

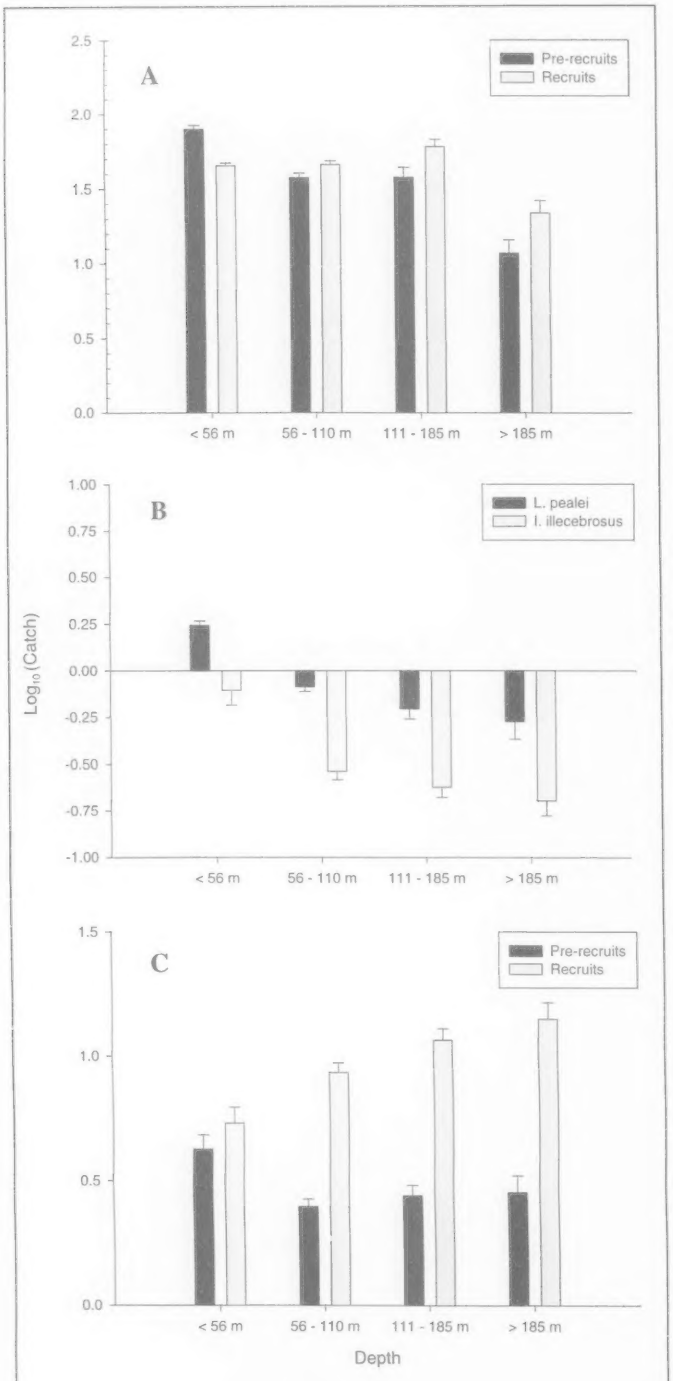

Figure 3

(**A**) Mean catch of *L. pealei*, (**B**) mean ratio of prerecruit to recruit catches, and (**C**) mean catch of *I. illecebrosus* by depth for positive catches of *L. pealei* and *I. illecebrosus* prerecruits and recruits.

For *I. illecebrosus*, the mean catch of prerecruits was highest during the day, whereas the mean catch of recruits peaked during dawn and dusk (Fig. 4C), where sample sizes for time zones I, II, and III were 86, 211, and 313 tows, respectively. Mean catches of prerecruits and recruits were lowest at night. For prerecruits, mean catches were not significantly different between time zones I and II (Fig. 4C). In contrast, mean catches of recruits were not significantly different between time zones II and III. Although the mean ratio of prerecruit to recruit catches peaked during the day (Fig. 4B), mean ratios were significantly different between time zones II and III. Similar to catches of *L. pealei*, catches of both size categories of *I. illecebrosus* were lowest at night.

Mean catches of *L. pealei* prerecruits and recruits differed by bottom temperature zone (Fig. 5A) where temperature zones I, II, and III were 5.5 to 10.9°C (n=604), 10.9 to 16.1°C (n=1,340), and 16.1 to 28.0°C (n=272), respectively. Mean catch of prerecruits increased with bottom temperature and peaked in the warmest zone, whereas mean catch of recruits was greatest in zones II and III. In contrast, the mean catches of both size categories were lowest in temperature zone I. Mean catches of prerecruits were significantly different between all bottom temperature zones (Fig. 5A), whereas mean catches of recruits were not significantly different between zones II and III. The mean ratio of prerecruit to recruit catch peaked in zone III (Fig. 5B), and the mean ratios were not significantly different between zones I and II. Overall, catches of *L. pealei* prerecruits increased with increasing bottom temperature, whereas catches of recruits peaked at intermediate levels (11–16°C).

Catches of *I. illecebrosus* prerecruits and recruits also varied (Fig. 5C) with bottom temperature, where zones I, II, and III were 5.1 to 10.2°C (n=122), 10.2 to 12.9°C (n=242), and 12.9 to 25.5°C (n=121), respectively. For *I. illecebrosus* prerecruits, mean catches were greatest in temperature zones I and II, and the mean catch of recruits peaked in zone II. Mean catches of *I. illecebrosus* prerecruits and recruits were lowest in temperature zones I and III,

respectively. For prerecruits, mean catches were significantly different only between temperature zones I and II (Fig. 5C), whereas mean catches of recruits were significantly different only between zones II and III. The mean ratio of prerecruit to recruit catches was greatest in temperature zones II and III (Fig. 5D), however there was no significant difference between the three zones. Overall, catches of *I. illecebrosus* prerecruits and recruits were relatively similar over the range of observed bottom temperatures (5–25°C).

Mean catches of *L. pealei* prerecruits and recruits differed with surface temperature (Fig. 6A) where temperature zones I, II, and III were 7.1 to 14.8°C (n=615), 14.8 to 20.9°C (n=1,178), and 20.9 to 28.3°C (n=460), respectively. Mean catches of prerecruits and recruits peaked in temperature zone II, whereas the lowest mean catch of prerecruits and recruits occurred in temperature zone I. Mean catches of both prerecruits and recruits were significantly different across all surface temperature zones (Fig. 6A). The mean ratio of prerecruit to recruit catches peaked in temperature zone II and the mean ratios were significantly different across all surface temperature zones (Fig. 6B). Overall, catches of *L. pealei* prerecruits and recruits peaked at intermediate surface temperatures (15–21°C).

Mean catches of *I. illecebrosus* prerecruits and recruits (Fig. 6C) also varied with surface temperature, where temperature zones I, II, and III were 7.8 to 14.4°C (n=123), 14.4 to 20.6°C (n=242), and 20.6 to 26.5°C (n=131), respectively. For *I. illecebrosus* prerecruits, mean catch peaked in temperature zone II but exhibited no trend across zones. In contrast, mean catch of recruits peaked in temperature zone III and exhibited an increasing trend with surface temperature. There were no significant differences in mean catch of prerecruits, by surface temperature zone (Fig. 6C), but mean catches of recruits were significantly different between temperature zones I and III. The mean ratio of prerecruit to recruit catch peaked in temperature zone I (Fig. 6D) and declined with increasing surface temperature. These mean ratios were significantly different between zones I and III. Over-

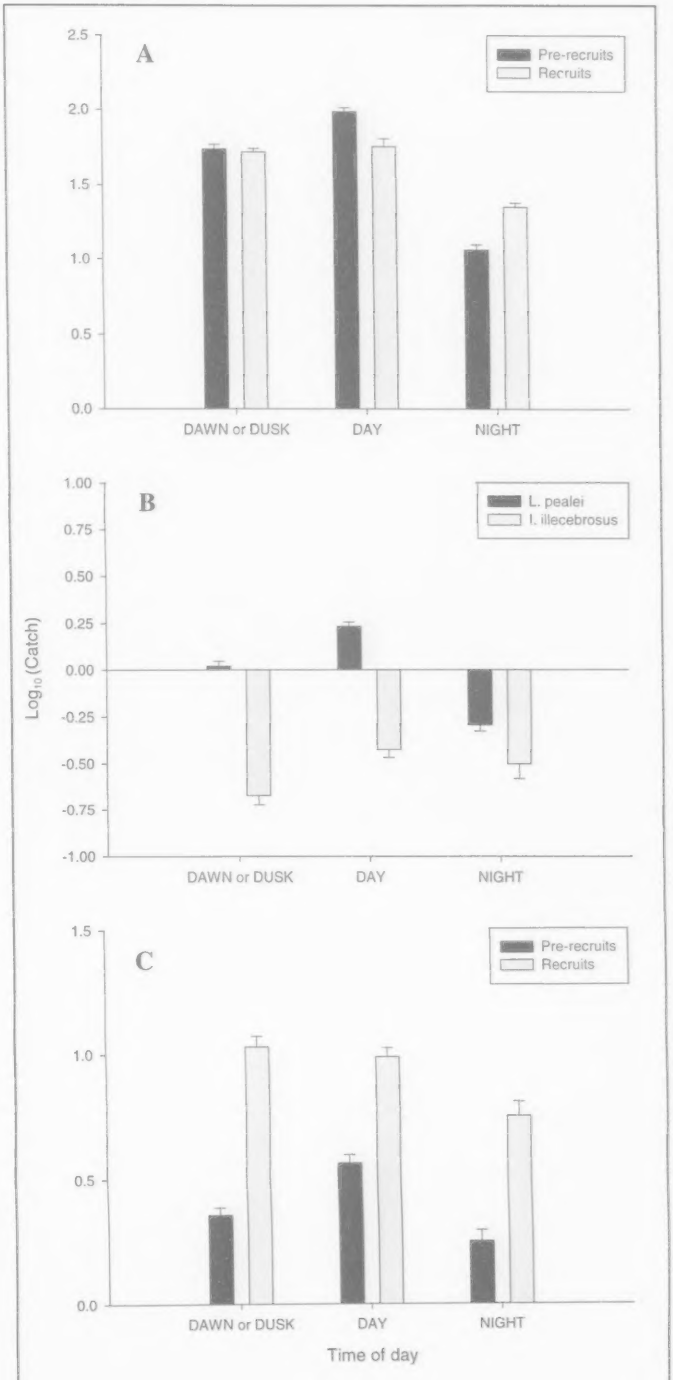

Figure 4

(**A**) Mean catch of *L. pealei*, (**B**) mean ratio of prerecruit to recruit catches, and (**C**) mean catch of *I. illecebrosus* by time of day for positive catches of *L. pealei* and *I. illecebrosus* prerecruits and recruits.

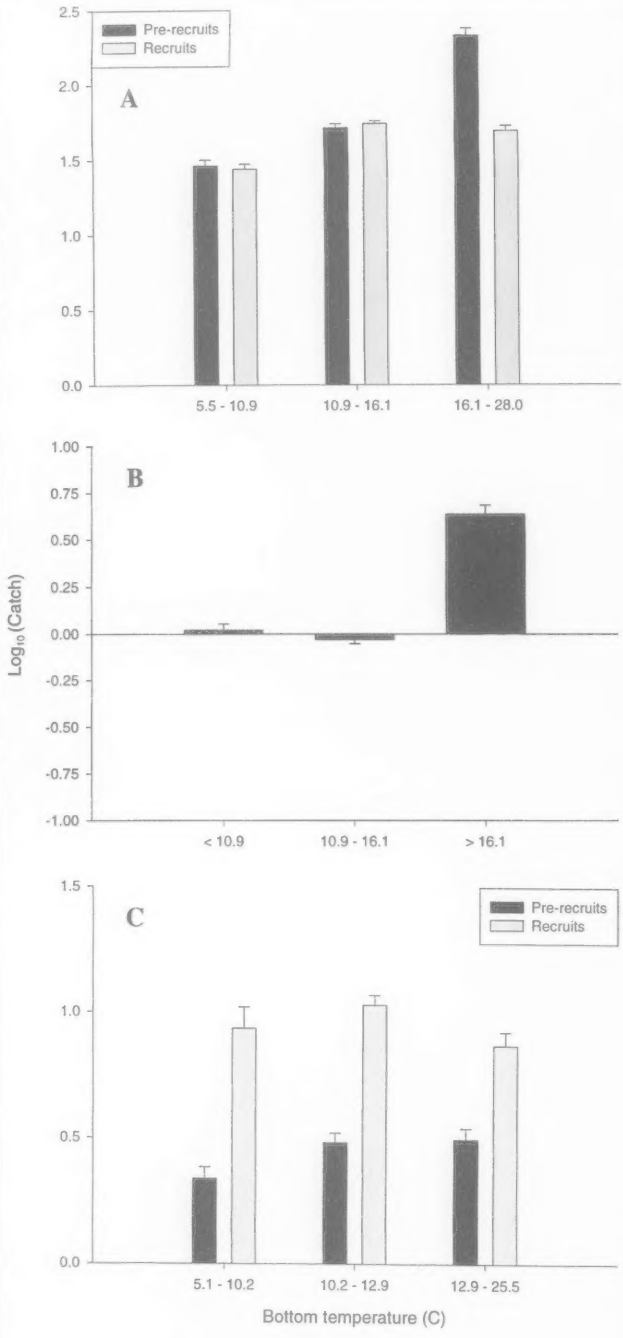

Figure 5

(**A**) Mean catch of *L. pealei*, (**B**) mean ratio of *L. pealei* prerecruit to recruit catches, (**C**) mean catch of *I. illecebrosus*, and (**D**) mean ratio of *I. illecebrosus* prerecruit to recruit catches by bottom temperature for positive catches of prerecruits and recruits.

all, catches of *I. illecebrosus* prerecruits were similar across the range of observed surface temperatures (8–26°C), whereas catches of recruits increased with surface temperature.

Diel correction factors

Diel effects from the GLM analyses were significant for *L. pealei* prerecruits and recruits and for *I. illecebrosus* prerecruits (Table 3). For *L. pealei* prerecruits, the time period effect was highly significant (F_S=280.79, P<0.001), and the year (F_S=6.05, P<0.001) and stratum effects (F_S=16.23, P<0.001) were also significant. Estimates of the diel effects coefficients for *L. pealei* prerecruits were T_I = 0.0873 with 95% CI of [0.0713, 0.1068] and T_{II} = 0.4654 with 95%CI of [0.3958, 0.5472]. For comparison, daytime catch rates of *L. pealei* prerecruits were roughly were about 11.5 times higher than time zone I values and 2.1 times higher than time zone II values. Similarly, for *L. pealei* recruits, the time period effect was highly significant (F_S=100.06, P<0.001), and the year (F_S=9.84, P<0.001) and stratum (F_S=12.45, P<0.001) effects were also significant. Estimates of the diel effects coefficients for *L. pealei* recruits were T_I = 0.3420 with 95% CI of [0.2939, 0.3979] and T_{II} = 0.8325 with 95%CI of [0.7372, 0.9402]. Time zone III catch rates of *L. pealei* recruits were roughly 2.9 times higher than time zone I values and about 1.2 times higher than zone II values. For *I. illecebrosus* prerecruits, the time period effect was significant (F_S=20.23, P<0.001). The stratum effect was also significant (F_S=1.98, P<0.001) but the year effect was not (F_S=1.48, P=0.057). Diel effects coefficients were estimated to be T_I = 0.4251 with 95% CI of [0.3158, 0.5724] and T_{II} = 0.6281 with 95%CI of [0.5093, 0.7746]. By comparison, time zone III catch rates of *I. illecebrosus* prerecruits were about 2.4 times higher than zone I values and roughly 1.6 times higher than time zone II values. For *I. illecebrosus* recruits, the time period effect was not significant (F_S=2.25, P=0.106), although the year (F_S=5.41, P<0.001) and stratum (F_S=3.05, P<0.001) effects were significant. For both species, diel effects were more pronounced for prerecruits than for recruits.

Discussion

We found that *L. pealei* was consistently associated with all the environmental factors examined. The habitat associations of *L. pealei* with depth, bottom temperature, and surface temperature indicated that these factors were important determinants of its autumn distribution. The consistent association of *L. pealei* with time of day appeared to be a consequence of the behavioral ecology of the species as it moves upward in the water column during the night to avoid predation or to acquire prey.

In comparison with *L. pealei*, autumn survey catches of *I. illecebrosus* were much lower and associations with environmental factors were inconsistent. For many of the years examined, *I. illecebrosus* catches were not associated with depth, temperature, or time of day. *Illex illecebrosus* feeds opportunistically in continental shelf waters from Newfoundland to Cape Hatteras, during summer and autumn, prior to undertaking a lengthy offshore migration to spawning areas south of Cape Hatteras (O'Dor and Dawe, in press). Therefore, the lack of consistent habitat associations may be partly due to incomplete survey coverage of *I. illecebrosus* habitat during autumn and a lack of availability of this species to the bottom trawl survey gear. For example, the timing of the offshore and southward migration of *I. illecebrosus* may precede rather than follow the timing of the autumn survey in some years. In addition, few stations are sampled in the autumn habitat of this species, at the shoreward edge of the convergence zone, and these low sample sizes may make it difficult to detect habitat associations. Nevertheless, *I. illecebrosus* catches were significantly associated with depth, time of day, and surface temperature in approximately half of the years examined. Depth and surface temperature may be determinants of preferred habitat of *I. Illecebrosus;* however the importance of these factors varied between years. The significant association of *I. illecebrosus* catches with daylight indicated that the species undertakes vertical migrations similar to those of *L. pealei*, but with less regularity as might be expected of an ommastrephid (Roper and Young, 1975).

Depth had an important effect on the magnitude of juvenile and adult *L. pealei* catches. This association with depth corroborated previous studies. Serchuk and Rathjen (1974) examined the distribution and relative abundance of *L. pealei* and found that the highest catches were at depths less than 100 m during autumn. Vovk (1978) reported that the primary depth range of *L. pealei* was 50–100 m during September–November, and Lange and Sissen-

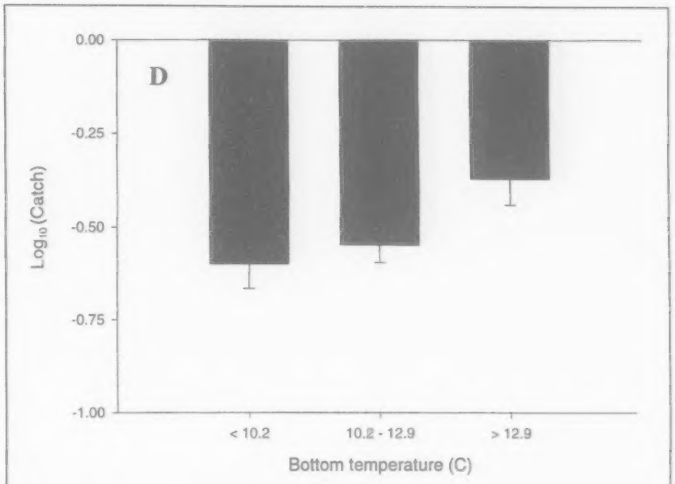

Figure 5 (continued)

Table 3

Analysis of variance tables for general linear model results to estimate diel correction factors for *L. pealei* and *I. illecebrosus* prerecruits and recruits, where df is degrees of freedom, SS is type-III sums of squares, MS is mean square, F_S is the *F*-statistic, and *P* is the probability value.

Source of variation	df	SS	MS	F_S	*P*
L. pealei prerecruits					
Year	27	104.824	3.882	6.05	<0.001
Stratum	50	520.624	10.413	16.23	<0.001
Time of day	2	360.353	180.176	280.79	<0.001
L. pealei recruits					
Year	27	96.171	3.562	9.84	<0.001
Stratum	50	225.257	4.505	12.45	<0.001
Time of day	2	72.439	36.220	100.06	<0.001
I. illecebrosus prerecruits					
Year	27	9.761	0.362	1.48	0.057
Stratum	50	24.114	0.482	1.98	<0.001
Time of day	2	9.866	4.933	20.23	<0.001
I. illecebrosus recruits					
Year	27	41.351	1.532	5.41	<0.001
Stratum	50	43.274	0.865	3.05	<0.001
Time of day	2	1.275	0.637	2.25	0.106

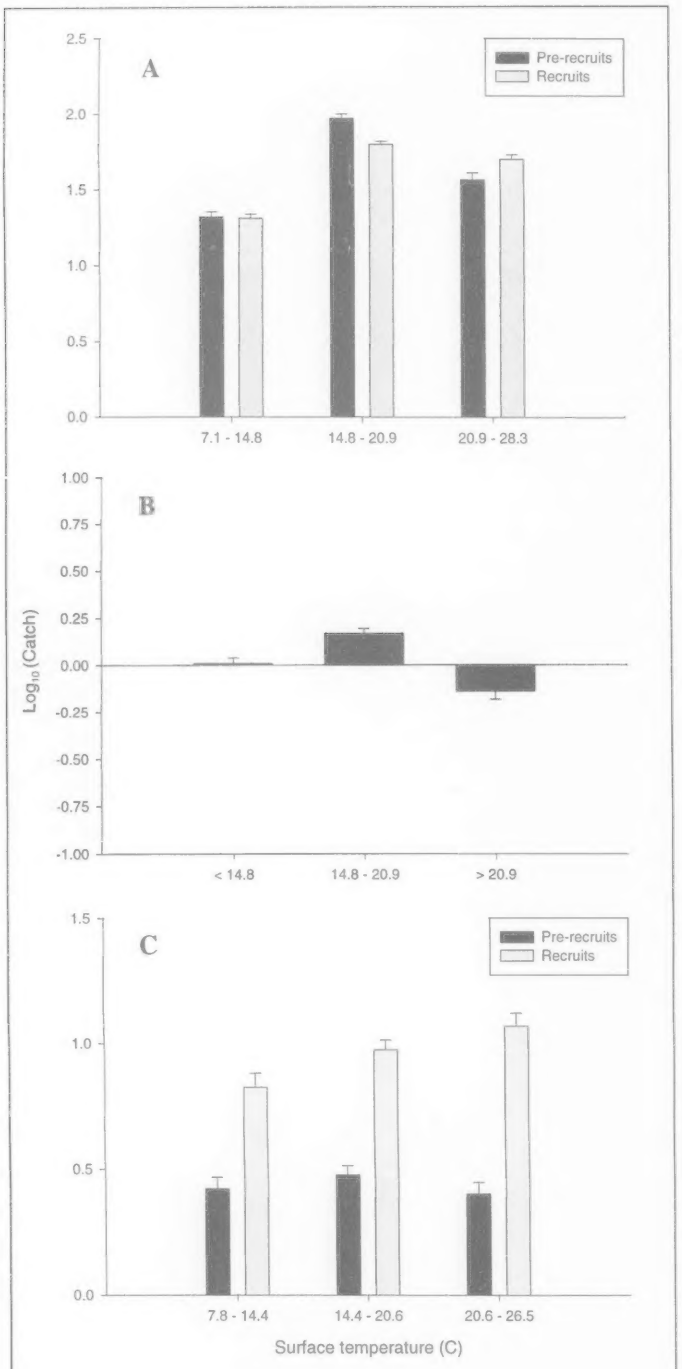

Figure 6

(**A**) Mean catch of *L. pealei*, (**B**) mean ratio of *L. pealei* prerecruit to recruit catches, (**C**) mean catch of *I. illecebrosus*, and (**D**) mean ratio of *I. illecebrosus* prerecruit to recruit catches by surface temperature for positive catches of prerecruits and recruits.

wine (1983) reported relatively high catches at shallow (27–55 m) and also intermediate depths (111–185 m). In this study, however, depth affected catches of juvenile and adult *L. pealei* differently. Most shallow-water catches comprised juveniles, and this finding indicated that nearshore waters of the continental shelf constitute a preferred habitat of *L. pealei* juveniles during autumn. Catches of juveniles also decreased at greater depths. In contrast, catches of *L. pealei* adults peaked at depths near the edge of the continental shelf. We detected a bathymetric pattern of larger *L. pealei* with increasing depth. This pattern was also reported by Vovk (1978) on the basis of distant water fleet catches of *L. pealei* and is similar to the ontogenetic descent reported for some other loliginids (*L. gahi*, Hatfield et al., 1990; *L. vulgaris reynaudii*, Augustyn et al., 1992).

In comparison with *L. pealei*, the effect of depth on *I. illecebrosus* was similar but less pronounced. This difference was probably due to the fact that *I. illecebrosus* utilize a wider range of depths than do *L. pealei* as they feed in shallow nearshore areas and undertake long distance migrations in continental slope waters (O' Dor and Dawe, in press). Nonetheless, the empirical patterns of *I. illecebrosus* catches in relation to depth in our study area were consistent with those from different areas. In particular, Whitaker (1980) reported that *I. illecebrosus* catches were relatively low at depths less than 56 m and peaked at depths between 186 and 366 m in waters south of Cape Hatteras, whereas Grinkov and Rikhter[3] reported that *I. illecebrosus* catches peaked at depths of 100–150 m along the edge of the continental shelf off Nova Scotia. In our study, much of the *I. illecebrosus* catch occurred at depths of roughly 80–150 m. As with *L. pealei*, we found that depth affected the catch of *I. illecebrosus* juveniles and adults differ-

[3] Grinkov, Y. A., and V. A. Rikhter. 1981. Some data on distribution of groundfish and shortfinned squid along the oceanic slopes of the Scotian Shelf in spring, 1979. Northwest Atlantic Fisheries Organization (NAFO) SCR Doc. 81/VI/63, ser. no. N347, 13 p.

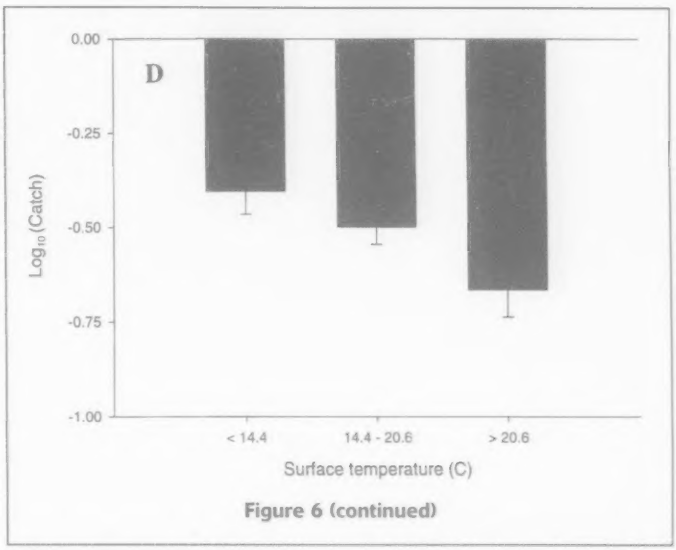

Figure 6 (continued)

ently. Catches of juveniles decreased at greater depths, and there was a bathymetric pattern of larger *I. illecebrosus* with increasing depth. Although catches of adults increased with depth, in contrast with *L. pealei*, catches of *I. illecebrosus* adults peaked at depths of 186–366 m. This depth range corresponds to the convergence zone between continental shelf and slope waters and intersects the shelf edge at roughly 150–200 m (Bowman, 1977). Commercial fishery catch data were consistent with this observation, as Lange, Ingham, and Price[4] reported, noting that the highest catch rates recorded by domestic observers in the distant-water *I. illecebrosus* fishery were generally located within several miles of the shelf-slope front, at the shoreward edge of the convergence zone, between continental shelf and slope water. Overall, these observations suggested that the shelf-slope convergence zone is an important habitat for adult *I. illecebrosus* during autumn.

Our analyses also demonstrated the importance of diel effects on *L. pealei* catches. This generally corroborated previous observations. Summers (1968) observed that *L. pealei* migrated vertically and that squid could be observed near the surface at night. Summers (1969) and Lange and Sissenwine (1983) observed that survey catches of *L. pealei* during the day were consistently higher than catches at night. Serchuk and Rathjen (1974) observed that 90% of *L. pealei* survey catches occurred during daylight, and Sissenwine and Bowman (1978) found that *L. pealei* catches were significantly higher during day. In our study, significant differences in diel effects were detected for both juveniles and adults. Catches of *L. pealei* juveniles and adults increased with increasing light availability although the diel effects were more pronounced for juveniles. In particular, time zone I and II catches of juveniles were 92% and 54% below mean catch during the day, whereas zone I and II catches of adults were 66% and 17% lower. The fact that the diel effect was more pronounced for juvenile *L. pealei* may be related to differences in feeding behavior between juveniles and adults. *L. pealei* hatchlings must feed near the surface until their tentacles develop and they can capture larger prey (Vecchione, 1981) whereas adults are primarily demersal and commonly rest on the bottom (Hanlon et al., 1983). Small juveniles feed primarily on crustaceans and gradually shift to a more diverse diet of crustaceans, fish, and squid as they grow and can capture larger and more energetically valuable prey (Vovk, 1972; Macy, 1982; Vovk, 1985; Anderson and Griswold, 1988). As a result, juveniles need to undertake vertical migrations at night more frequently to capture a sufficient amount of suitable prey.

The fact that *I. illecebrosus* catches were moderately associated with time of day was consistent with Sissenwine and Bowman (1978) and Shepherd and Forrester[2] who found that time of day had an important effect on catches of *I. illecebrosus*. Diel vertical migrations may be related to *I. illecebrosus* feeding activity. Vinogradov and Noskov (1979) found that the feeding intensity of this species is greatest at night and lowest during the day. Similar to catches of *L. pealei*, catches of *I. illecebrosus* were higher during day, and diel effects were more important for juveniles than adults. In particular, catches of juveniles at night and those at dawn and dusk were 37% and 57% below mean catch during the day. Guided by a review of the NEFSC domestic sea sampling program database, fishermen targeting *I. illecebrosus* take advantage of the behavior of this species by fishing only between dawn and dusk, when the squid are available to commercial bottom trawl gear. Schools of *I. illecebrosus* are not targeted at night because they are too dispersed near the surface of the water column. Instead schools of *I. illecebrosus* are targeted beginning at dawn, when they can be

[4] Lange, A. M. T., M. C. Ingham, and C. A. Price. 1984. Distribution of maturing *Illex illecebrosus* relative to the shelf-slope water front of the northeastern United States. NAFO SCR Doc. 84/IX/109, Ser. No. N906, 18 p.

consistently seen on sonar returning to the seabed.[5] In contrast, the ratios of juvenile to adult catches of *I. illecebrosus* were considerably lower than those for *L. pealei*. In part, this difference in ratios between species may reflect the importance of cannibalism for larger *I. illecebrosus* adults during autumn (O'Dor and Dawe, in press). Although diel effects on *I. illecebrosus* juvenile catches were similar to *L. pealei*, they were less consistent.

We found that bottom temperature had a significant effect on catches of *L. pealei* juveniles and adults. This generally corroborated prior studies. In particular, Summers (1969) observed that large catches of *L. pealei* during winter were restricted to bottom temperatures of 8°C or higher. This lower temperature limitation was supported by Serchuk and Rathjen (1974) and Vovk (1978) who reported that the majority of *L. pealei* catches during autumn occurred at bottom temperatures of roughly 9–14°C. Similarly, in our study, much of the *L. pealei* catch occurred at 11–15°C. However, catches of *L. pealei* juveniles were highest when bottom temperatures exceeded 16°C, whereas catches of adults were highest when bottom temperatures were 11–16°C. Our results suggest that *L. pealei* juveniles generally prefer warmer bottom temperatures than do adults that appear to prefer intermediate bottom temperatures. This difference in temperature preference might be expected if minor differences in temperature have a substantial impact upon growth rates of young squid (Forsythe, 1993).

In contrast to bottom temperature, catches of *L. pealei* juveniles and adults had a similar pattern with respect to surface temperature. The highest catches of both *L. pealei* juveniles and adults occurred at temperatures of 15–21°C, whereas catches were lowest for temperatures below 15°C. Although *L. pealei* catches might be expected to increase with warmer water temperatures, adult catches peaked at intermediate bottom and surface temperatures and then declined at higher temperatures. This decline suggested that the higher temperature ranges observed in the survey were not optimal for *L. pealei* adults. Overall, the strong association of *L. pealei* with water temperature suggested that annual variation in patterns of ocean temperature affects the distribution and influences growth and survival of this neritic species.

In comparison to *L. pealei*, the less frequent associations of *I. illecebrosus* catches with bottom and surface temperatures suggested that temperature has a variable influence on the distribution of *I. illecebrosus* from Cape Hatteras to the Gulf of Maine. Other studies generally supported the notion that *I. illecebrosus* are distributed over a broad range of temperatures. In particular, Whitaker (1980) reported that *I. illecebrosus* catches occurred over a wide range of bottom temperatures of 7–27°C, but that roughly 80% of the catch was taken in 8–10°C waters. Murawksi (1993) examined the mean latitudinal occurrence of *I. illecebrosus* in relation to bottom and surface temperatures during autumn NEFSC bottom trawl surveys but found no statistically significant relationship. Rowell et al. (1985b) reported that *I. illecebrosus* appear to prefer bottom temperatures in excess of 6°C during summer on the Scotian Shelf, but that temperature did not appear to be a limiting factor. In the present study, much of the *I. illecebrosus* catch occurred at bottom temperatures of 9–13°C and surface temperatures of 13–20°C. In comparison to *L. pealei*, *I. illecebrosus* appeared to prefer cooler bottom temperatures and surface temperatures. However, in contrast with *L. pealei*, bottom temperature had a similar affect on catches of juvenile and adult *I. illecebrosus*. Surface temperature affected catches of juveniles and adults differently and, in particular, adult *I. illecebrosus* catches increased with surface temperature. Overall, *I. illecebrosus* catches occurred over a broader range of water temperatures in comparison with *L. pealei*, as might be expected of an oceanic species with a range that extends from temperate to boreal waters.

Because the bottom trawl gear used on the NEFSC autumn survey only fishes 3.2 m above the seabed, diel differences in squid catches are expected when squid migrate vertically to acquire prey or to avoid predators. Significant differences were detected between catches by time of day for both juvenile and adult *L. pealei*. As a consequence, it was inferred that diel correction factors were appropriate for survey catches of this neritic species. In contrast, diel effects on survey catches of adult *I. illecebrosus* were not significant and diel correction factors were not developed for this oceanic species. The diel catchability of *L. pealei* presents some challenges for the analysis and interpretation of bottom trawl survey data to estimate squid population totals. On one hand, diel correction factors developed in this study can be applied to time zone I and II catches to provide a stratified mean catch per tow adjusted to daylight units. Resampling techniques, such as mirror-match bootstrapping, could be applied to estimate its variance (Smith, 1997) under appropriate distributional assumptions. In this case, all survey data could be used at the expense of additional computational cost and potential bias induced by applying the diel correction factors to all survey strata. On

[5] Goodwin, G. 1997. Captain of *F/V Relentless* and *F/V Persistence*. Davisville, Rhode Island, 02882. Personal commun.

the other hand, squid population size and its variance could be calculated on the basis of only daylight tows in the standard manner. In this case, roughly 1/3 of the available survey data would be used owing to the exclusion of time zone I and II tows. As a result, some survey strata would be undersampled and precision would be lower. In general, the trade-off between bias due to diel correction and loss of precision due to use of only daylight tows warrants further study.

Differences between *L. pealei* and *I. illecebrosus* catches by depth suggest that the stratification of the NEFSC bottom trawl survey, which was designed to sample groundfish populations, is appropriate for both species. Differences in *L. pealei* and *I. illecebrosus* catches by temperature imply that preferred temperature ranges likely exist for both species within the survey region. However, temperature would not be a useful stratification variable for analysis of squid catches because temperature strata are dynamic and would fluctuate each year and because such a variable would lead to overstratification given the current depth and geographic stratification of the NEFSC survey. Regardless of how temperature affects survey catches of squids, the growth, recruitment, and abundance of *L. pealei* and *I. illecebrosus* can be expected to vary with ocean temperature regime (e.g. Dawe and Warren, 1993; Brodziak and Macy, 1996) because both are ecological opportunists with high, intrinsic population growth rates. Understanding how environmental factors, such as temperature, influence the productivity and distribution of squid stocks remains an important topic for fisheries research and management.

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Modeling the dynamics of eastern rock lobster, *Jasus verreauxi*, stock in New South Wales, Australia

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Abstract.—Rock lobster, *Jasus verreauxi*, have been fished off New South Wales, Australia, since the late nineteenth century. Since 1994–95 (1 July 1994 to 30 June 1995) the fishery has been managed under an output-control scheme with an annual total allowable catch (TAC) of 106 metric tons (t). Estimates of catch and catch per unit of effort (CPUE) have been developed from data collected from the commercial fishery for the period 1903–1936 and the period from 1969–70 to 1993–94. A production model was fitted to these data by using a robust observation-error estimator that minimizes the median of squared differences between log-observed and predicted CPUEs. A bootstrap resampling procedure was incorporated into this robust estimation method to estimate stock parameters and their uncertainties. The virgin biomass of the rock lobster was 4084 t (its 5th and 95th percentiles being 2553 and 6400 t). The stock biomass decreased substantially until 1990–91. Since 1992–93, it has stabilized and has probably increased owing to the large decrease in the allowable catch after 1988–89. The stock biomass in year 1995–96 was likely to have been between 15% and 30% of the virgin biomass (75% confidence interval). The implications from using different estimation methods on assessing this lobster stock are discussed.

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The eastern rock lobster, *Jasus verreauxi*, reportedly is the largest spiny rock lobster in the world (Philips et al., 1980). It occurs in waters off the coast of New South Wales (NSW), Australia, around the coast of Tasmania, and as far west as South Australia (Montgomery, 1995). It is also found off New Zealand, predominantly around the North Island (Kensler, 1967a).

Limited information on the life history of *J. verreauxi* in waters off NSW is available (McWilliam and Philips, 1987; Montgomery, 1992, 1995; Montgomery and Kittaka, 1994; Montgomery[1]). Most information comes from studies of the species in waters off New Zealand (Kensler 1967a, 1967b, 1967c; Booth, 1984a, 1984b, 1986). However, comparisons of mitochondrial DNA from juvenile rock lobsters from NSW and New Zealand waters have suggested that the populations are genetically distinct (Brasher et al., 1992).

The distribution of rock lobsters across habitat is patchy. From the puerulus to early juvenile stages of their life cycle, lobsters are probably asocial and thought to occur principally within the complex structure of forests of macroalgae or within beds of seagrass in waters from the intertidal zone to 30 m. During the older stages of the juvenile phase, the animal may begin to aggregate and migrate en masse to the habitat of adults. Adult rock lobsters live in aggregations from depths of around 10 m to those of the continental slope (Montgomery, 1995; Montgomery[1]). From the older juvenile stage onward, lobsters aggregate by day, and at night they roam alone. Information on the movements of tagged rock lobsters off New Zealand (Booth, 1984b) and spatial patterns in the length composition of rock lobsters in waters off NSW (Montgomery[1]) suggest that for management purposes the entire NSW population of rock lobsters should be considered as a unit stock. These studies indicate that older juveniles and adults move in an inshore–offshore direction and along the coast. The movement along the coast is thought to be associated with breeding (Booth, 1984b).

Rock lobsters have been fished off the east coast of Australia since the late nineteenth century. It is an important fishery in NSW, with an annual output of over 5 million US dollars. Since the 1994–95 fishing

[1] Montgomery, S. S. 1990. Preliminary study of the fishery for rock lobsters off the coast of New South Wales. Final Report, grant no. 86/64. Fisheries Research and Development Corporation, Canberra, Australia, 166 p.

year (i.e. from July 1 1994 to June 30 1995), this fishery has been managed under an output-control scheme with an annual total allowable catch (TAC) of 106 t. No attempt has been made previously to quantify the dynamics of this fishery.

Abundance indices, catch per unit of effort (CPUE), have been developed by Montgomery (1995) from data collected in the commercial fishery for the period of 1903–36 and that from 1969–70 (i.e. 1 July 1969 to 30 June 1970) to 1993–94. Because data are mainly collected and derived from the NSW commercial fishery, large errors are likely to exist in the catch and CPUE data, and there is a concern that the quality of the data is perhaps not good for the purpose of modeling.

Production models are fitted to catch and CPUE data by using an observation-error estimator that minimizes the sum of squared differences between log-observed and predicted CPUEs (Hilborn and Walters, 1992). This estimator assumes that there is only error in the observed abundance index and that there are no observation errors in catch or process errors in the dynamics of the stock biomass. Because the least-squares method is sensitive to the assumption on the error structure in the model (Rousseeuw and Leroy, 1987), the unrealistic error assumption associated with the observation-error estimator tends to result in large errors in estimated parameters when models are fitted to data (Schnute, 1989; Chen and Andrew, 1998).

A more realistic error structure should include process error in the dynamics of the stock biomass and observation errors in both CPUE and catch. In our case, if the distribution of all error terms can be fully defined, we can apply the Kalman filter to generate a likelihood function and then maximize this likelihood function to yield parameter estimates (Sullivan, 1992), or we can define an appropriate variance-covariance matrix based on the defined error structure and then apply a generalized least-squares method to estimate parameters in the model (Paloheimo and Chen, 1996). However, the former approach is rather complicated because the dynamic model is nonlinear and there are two observation models (i.e. one for CPUE and the other for catch; Reed and Simons, 1996). The latter approach needs information on process and observation errors (Paloheimo and Chen, 1996). Such information is probably nonexistent in most fisheries. Moreover, the parametric assumption on error distribution (e.g. normal, log-normal, etc) may not be true.

Because of all these difficulties with the error structure for production models, it is desirable to have an estimation method that is robust with respect to assumptions concerning model error structure. Least median of squared errors (LMSE; Rousseeuw, 1984), which minimizes the median of squared differences between predicted and observed log CPUEs, is such an estimator (Chen and Andrew, 1998). A bootstrap procedure (Efron, 1979) was incorporated into the LMSE estimator to estimate the parameters and their uncertainties in this study. The probability of short-term overexploitation, defined as a fishing mortality rate higher than the selected biological reference points, was estimated for the next fishing season with different levels of TAC.

Production models

Production models are the simplest stock assessment models that are commonly used in fisheries (Hilborn and Walters, 1992). The input data for these models are the time series of catch and associated abundance index. Several variants of production models have been proposed (e.g. Pella and Tomlinson, 1969; Walters and Hilborn, 1976; Schnute, 1977, 1989; Punt, 1993). Without considering the structure of observation and process errors, the deterministic production model that is most commonly used can be written as

$$B_{i+1} = B_i + g_i - C_i, \quad (1)$$

where B_i = the stock biomass;
C_i = the catch; and
g_i = the growth of population in biomass, all in year i.

The g_i is often referred to as surplus production and often described by the logistic or Schaefer function written as $g(B_i) = rB_i(1 - B_i/K)$, where r is a parameter describing the intrinsic rate of population growth in biomass and K is a parameter corresponding to the unfished equilibrium stock size (often referred to as the carrying capacity or virgin biomass). The stock biomass in year i is often assumed to be directly related to a relative abundance index that can be observed in fisheries. This assumption can be written as

$$I_i = qB_i,$$

where q = the catchability coefficient; and
I_i = the abundance index in year i (Hilborn and Waters, 1992).

Methods for the parameter estimation

The use of an appropriate method to fit a production model to the observed data has been shown to be as

important in terms of the reliability of estimated parameters as the specification of the algebraic form of the underlying population dynamic model (Punt, 1988, 1993; Polacheck et al., 1993). Several approaches have been proposed to estimate parameters in production models when only indices of abundance and catch are available (Hilborn and Walters, 1992). The four most commonly used approaches are equilibrium estimators (Gulland, 1961), effort-averaging estimators (Fox, 1975), process-error estimators (Walters and Hilborn, 1976; Schnute, 1977), and observation-error estimators (Butterworth and Andrew, 1984; Ludwig and Walters, 1985). These approaches differ in how observation and process errors are introduced into the models that describe the dynamics of populations.

Recently, it has been suggested in some studies that observation-error estimators tend to perform better than others in parameter estimation (Punt, 1988, 1993; Hilborn and Walters, 1992; Polacheck et al., 1993). These estimators are constructed by assuming that the population dynamic equations are deterministic (thus there is no process error) and that all of the error occurs in the relationship between stock biomass and relative abundance index. This assumption can be written as

$$\log(I_i) = \log(qB_i) + e_i.$$

With the assumption that the e_i are independent, normally distributed variates, the estimates of the model parameters ($B_{initial}$, q, r, and K) are obtained by maximizing the appropriate likelihood function (Polacheck et al., 1993) or by minimizing the sum of squared e_i (Hilborn and Walters, 1992). The time series of stock biomass are estimated by projecting the biomass at the start of the catch series forward by using the historical annual catches. Because the estimation methods for observation-error estimators are least-squares types, they are sensitive to the assumption about the error structure of the model. Thus, parameter estimates tend to be unreliable if the specification of error structure (i.e. no process error, no error in observed catch, and log-normal error in observed abundance index) is not correct. However, in practice, it is almost impossible to know the true error structure. It is therefore desirable to use an estimation approach that is robust to the assumption about the model error structure for observation-error estimators.

An observation-error estimator, which minimizes the median of squared differences between observed and predicted log CPUEs, has been found to be robust with respect to incorrect specification of error structure (Chen and Andrew, 1998). This estimator can be written as

$$Minimize \underset{i=1,\ldots,N}{median} \left[\log(I_i) - \log(\hat{I}_i)\right]^2.$$

It is an extension of the linear robust regression method used by Chen and Paloheimo (1994) and Chen et al.(1994) for nonlinear parameter estimation. It should be noted that the algorithm developed for the linear parameter estimation (Rousseeuw, 1984) can not be used for the above estimator. The simplex method of Nelder and Mead (1965) was used to conduct the nonlinear parameter estimation for the above estimator (Press et al., 1992; Chen and Andrew, 1998).

Estimation of stock parameters for eastern rock lobster

Catch and CPUE data were available for two time periods. The first period (hereafter referred to as period I) was from 1903 to 1936, and the second (period II) from 1969–70 to 1993–94. The fishery was confined to grounds close to shore in period I, whereas from the beginning of period II, the fishery expanded to the continental slope. Therefore, it is highly likely that large differences in catchability existed between these two periods. Both the size and structure of the rock lobster stock on the NSW coast may have changed greatly over the two periods (Montgomery, 1995), and it is likely that the growth rate of the NSW rock lobster stock differed between these two periods of time. Parameters r and q were thus assumed to be different in these two time periods. Parameter K was assumed to be the same for these two time periods. This assumption was considered to be reasonable because the harvesting on the expanded fishing grounds at the beginning of period II was not from an unexploited portion of the stock. It is thought that eastern rock lobsters along the NSW coast display a movement that is typical of several other species of rock lobster, moving between inshore and offshore grounds and along the coast (see Herrnkind et al., 1994). Hence, lobsters on the grounds on the continental slope likely had been exposed to fishing on more traditional shallower grounds at other times.

The LMSE method was applied to fit the model to data observed in period I and estimate parameters B_{1903}, r_I, q_I, and K_I, where subscript I refers to period I. Because the year 1903 was early in the development of the fishery, it is reasonable to assume that B_{1903} is the same as K_I in parameter estimation (Hilborn and Walters, 1992). Thus, there are only three parameters to be estimated with data observed in the first time period.

An algorithm that incorporates a bootstrap approach into the LMSE method was developed to es-

timate the sampling distribution for model parameters. This approach is referred to as the bootstrapped LMSE method and its precedure follows:

1 estimate the model parameters using the LMSE method;
2 calculate the predicted CPUEs using the LMSE-estimated parameters;
3 calculate the residuals between observed and predicted log CPUEs;
4 randomly sample the residuals with replacement to add to the predicted logarithm CPUEs to yield pseudo observed CPUEs;
5 apply the LMSE algorithm to the pseudo observed CPUEs to estimate bootstrapped estimates;
6 repeat steps 4 to 5 100 times to simulate 100 sets of pseudo CPUE data and to estimate subsequently the corresponding 100 sets of bootstrapped parameters; and
7 calculate the median value and 90% confidence intervals for each parameter using the 100 bootstrapped estimates.

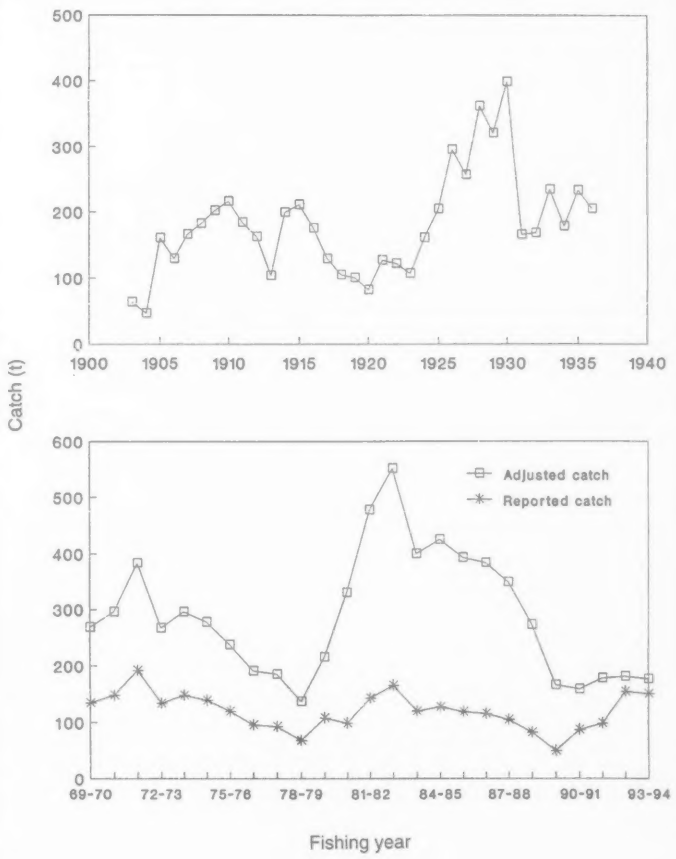

Figure 1

The landed catch of eastern rock lobsters in New South Wales (NSW), Australia, during the period of 1903–36, and from 1969–70 (i.e. 1 July 1969 to 30 June 1970) to 1993–94.

Following Efron and Tibshirani (1985) and Manly (1991), the median values and 90% confidence intervals derived from the 100 sets of bootstrapped parameters were used as the parameter estimates and their associated uncertainties. The 100 bootstrap runs were considered sufficient for the LMSE method in this study because a preliminary analysis indicated that differences in the distributions of estimated parameters derived from 100 and 2000 bootstrap runs were small.

Since K_{II} was assumed to be the same as K_I, there were three parameters, r_{II}, q_{II}, and B_{69-70}, to be estimated in modelling CPUE and catch data observed in period II. Although CPUE for period II was derived from accurate records of catch and effort associated with part of the commercial fishery, under-reporting of total catch occurred to a significant extent during period II (Montgomery and Chen, 1996). The extent of under-reporting in different fishing seasons was estimated on the basis of a survey of fishermen (Table 1; Montgomery[1]; Montgomery, unpubl. data). Thus, catch in fishing year j was adjusted from the reported catch (Fig. 1) as

$$(Adjusted\,catch)_j = \frac{(reported\,catch)_j}{1-(adjustment\,coefficient)_j},$$

where adjustment coefficient = the proportion of under-reporting estimated.

The seven-step procedure described above was modified to include the uncertainties in K_I in estimating the parameters and associated uncertainties in period II. The modification was accomplished by using values of K_I randomly sampled from the bootstrapped samples generated in the bootstrapped LMSE analysis for period I. Such a modification takes into consideration the variation in K_I (thus K_{II}) when estimating q_{II}, r_{II}, and $B_{1969-70}$ and their variabilities.

Table 1

Coefficients used to adjust reported catch data in the period of 1969–70 to 1993–94.

Year	Adjustment coefficient
1969–70 to 1979–80	0.5
1980–81 to 1989–90	0.7
1990–91 to 1991–92	0.45
1992–93 to 1993–94	0.15

Evaluation of probability of overexploitation for next fishing season

The probability of short-term overexploitation (i.e. the probability of the fishing mortality rate being higher than defined biological reference points) was defined with respect to different levels of catch for the 1996–97 fishing season. The two biological reference points used in our study were $f_{0.1}$ and f_{MSY}. The $f_{0.1}$ is equivalent to the more commonly used $F_{0.1}$ (Hilborn and Walters, 1992) and is defined by the equation

$$\left.\frac{\partial C(E)}{\partial E}\right|_{E=f_{0.1}q} = 0.1\left.\frac{\partial C(E)}{\partial E}\right|_{E=0},$$

where $C(E)$ = the equilibrium yield corresponding to effort E (Punt, 1993).

From the above equation and Equation 1, $f_{0.1}$ can be calculated as $f_{0.1} = 0.45r$. The TAC in year j based on the $f_{0.1}$ can be calculated as $TAC_{0.1}(j) = 0.45rB_j$, where B_j is the estimate of stock biomass in year j. The rate of fishing mortality (f_{MSY}) producing maximum sustainable yield (MSY) can be calculated as $f_{MSY} = 0.5r$. The TAC in year j, based on f_{MSY}, can be calculated as $TAC_{MSY}(j) = 0.5rB_j$. It should be noted that the $TAC_{MSY}(j)$ calculated above changes with the current stock biomass and is thus dynamic over time. It differs from the commonly used equilibrium maximum sustainable yield (EMSY) calculated as $rK/4$ (Hilborn and Walters, 1992). The use of $TAC_{MSY}(j)$ is more robust with respect to interannual variability in the biomass of the stock than is a TAC based on the more commonly used EMSY.

Results

Parameters r_I, q_I, and K_I estimated with the LMSE method were 0.203, 1.76×10^{-6} (per vessel, and 3208 t, respectively. This results in an EMSY of 163 t. The predicted CPUEs tended to follow the CPUEs observed in the majority of years in period I (Fig. 2). However, CPUEs observed in the years 1904 and 1917–24 differed considerably from the LMSE-predicted values, indicating that they virtually were ignored in the parameter estimation. The estimated stock size in year 1936 was 37.6% of the virgin biomass. The median value for K_I from the 100 bootstrapped LMSE estimates was 4084 t (Table 2), about 27% higher than the LMSE-estimated K_I. The coefficient of variation (CV) for the LMSE-estimated K_I was only 26%, indicating that the uncertainty associated with the LMSE-estimated K_I was small. The median values of bootstrapped r and q were 0.155 and 1.2×10^{-6} (per vessel) (Table 2), about 24% and 32% lower than the LMSE-estimated r and q, respectively. The higher CV for r, compared with the CVs for q and K_I, indicates that the estimate of r is more uncertain than the estimates of q and K_I. The distributions of all three parameters tended to be positively skewed (Fig. 3). The estimated EMSY ranged from 50 t to 200 t with the median value of 151 t (Fig. 3).

By assuming K_{II} to be the same as the median value of K_I estimated in the bootstrapped LMSE estimation, we estimated parameters r_{II}, q_{II}, and $B_{1969\text{–}70}$. The LMSE-estimated $B_{1969\text{–}70}$ was close to the value of K_I (4,365 t). The r_{II} was 0.218, about 7% higher than the LMSE-estimated r_I. The LMSE-estimated q_{II} was 0.15 $\times 10^{-6}$ (per trap-month). The model was fitted by means of the LMSE method by ignoring the data observed in the two fishing seasons 1971–72 and 1974–75 because

Table 2

Summary of the estimates of parameters with the bootstrapped LMSE method from 100 runs of bootstrap simulation for CPUE and catch data observed during 1903 to 1936.

	Parameter			
Statistic	r_I	$q_I \times 10^{-6}$ (per vessel)	K_I	σ^1
Median	0.155	1.20	4084	0.428
Mean	0.149	1.26	4269	0.497
CV	48.6%	28.0%	26.0%	53.1%
5th%	0.045	0.79	2554	0.187
95th%	0.292	1.94	6400	1.058

[1] For each bootstrap run, σ is calculated as

$$\sigma = \sqrt{\frac{\sum_{j=1}^{n}(CPUE_j - \hat{CPUE}_j)^2}{n}},$$

where CPUE and $\hat{CPUE}$ are observed and predicted catch per unit of effort, respectively, and n is the number of years.

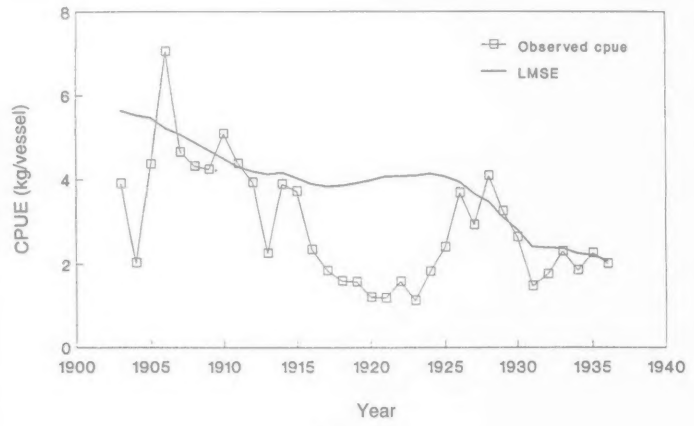

Figure 2

Catch per unit of effort observed and predicted by the LMSE method for the NSW eastern rock lobster fishery in the period of 1903 to 1936.

CPUEs in these two fishing seasons increased greatly and abruptly from the previous years, followed by an equally abrupt decrease (Fig. 4).

Distributions for parameters of the model estimated with the bootstrapped LMSE method for period II are presented in Figure 5. The median value of the stock biomass in year 1969–70 was 3808 t, 13% lower than the corresponding LMSE estimate. The estimated median value of r_{II} was 0.172 (Table 3), 22% lower than the LMSE-estimated r_{II}. The median value of q_{II} was only 10% of that estimated for q_I. This resulted from different units of fishing efforts used in calculating the abundance index (CPUE) in the two

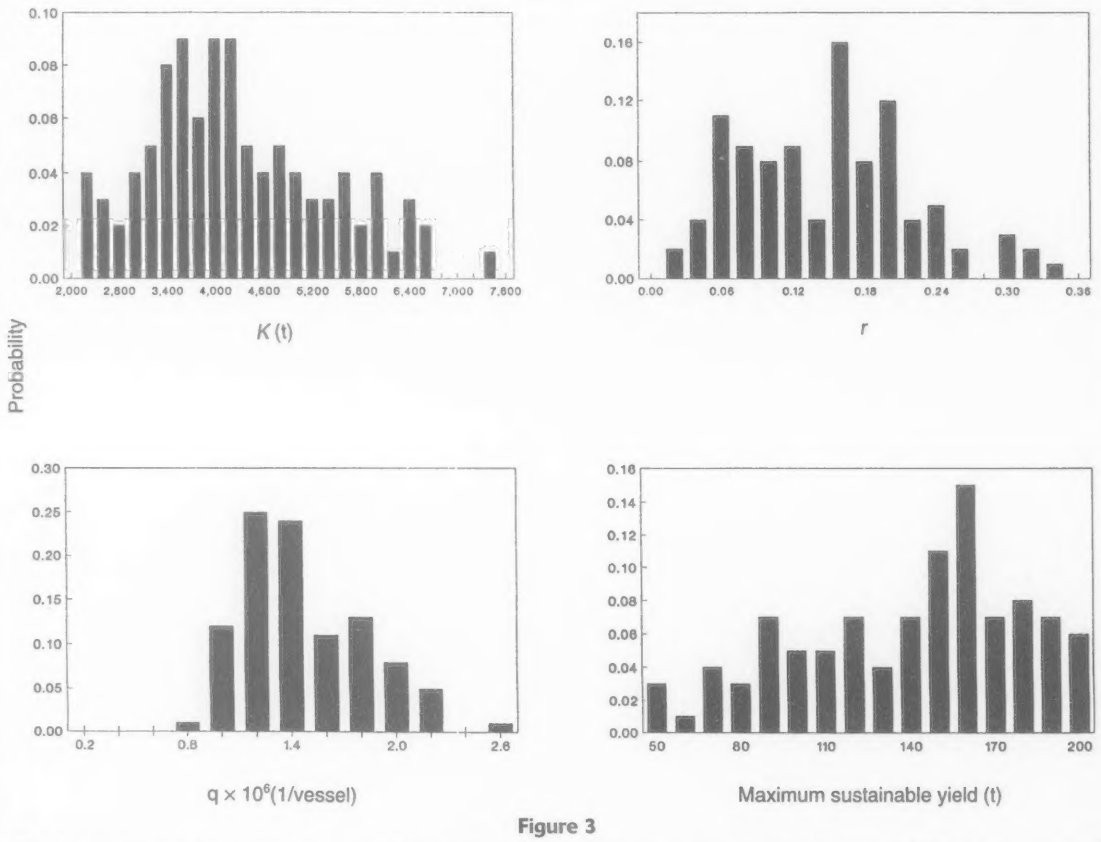

Figure 3

The distributions of the parameters estimated with the bootstrapped least median of squared errors (LMSE) for the period of 1903 to 1936.

time periods (per vessel versus per trap-month). The CVs and 90% confidence intervals for the parameters were small (Table 3), indicating that estimates of parameters for period II had small uncertainties. The estimated EMSY ranged from 80 t to over 200 t with a median value of 120 t (Fig. 5).

The median and 5th and 95th percentiles of the biomass of the stock for each year in period II are plotted in Figure 6. The calculation of total catches for 1994–95 and 1995–96 had not been completed when this study was conducted. However, the TAC of 106 t was likely to have been fully realized in each of these years. Thus, the biomasses of the stock for 1995–96 and 1996–97 were projected based upon the assumption that catches in 1994–95 and 1995-96 were 106 t. The 90% confidence intervals tended to increase from 1969–70 to 1994–95 (Fig. 6), indicating that estimates of the stock biomass in recent years were less precise than those in earlier years. The median value of the biomass of stock in the 1995–96 fishing year was 1420 t, and the 5th and 95th percentiles were 710 and 2719 t (Fig. 6). Median values for the biomass of the stock fell until 1990–91 and then started to increase from 1992–93. The plot of the distribution of the ratio between biomass in year 1995–96 against the biomass of the virgin stock indicated that there was more than 75% chance that the biomass ranged between 15% and 30% of the virgin biomass (Fig. 7).

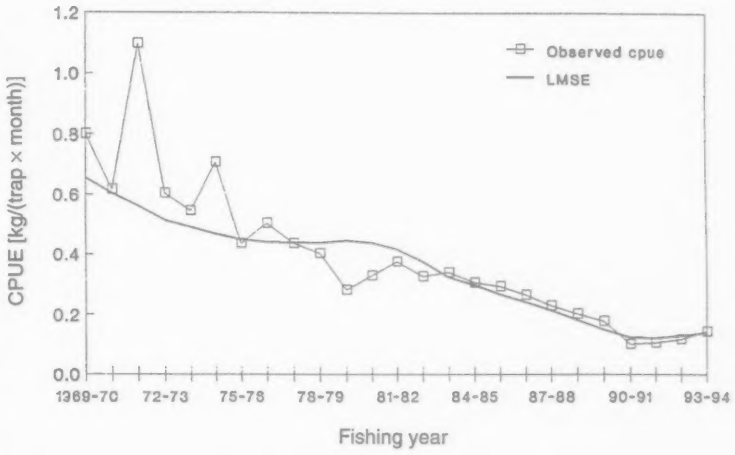

Figure 4

Catch per unit of effort observed and predicted with the LMSE method for the NSW eastern rock lobster fishery during the period of 1969–70 (i.e. 1 July 1969 to 30 June 1970) to 1993–94 (i.e. 1 July 1993 to 30 June 1994).

Table 3

Summary of the estimates of parameters using the LMSE method from 100 runs of bootstrap simulation for CPUE and catch data observed from 1969–70 to 1993–94.

	Parameter			
Statistic	r_{II}	$q_{II} \times 10^{-6}$ (trap × month)$^{-1}$	$B_{1969-70}$ (ton)	σ^1
Median	0.172	0.15	3808	0.237
Mean	0.177	0.15	3764	0.241
CV	19.4%	16.2%	11.5%	360%
5th%	0.132	0.11	3099	0.059
95th%	0.223	0.18	4418	1.098

[1] For each bootstrap run, σ is calculated as

$$\sigma = \sqrt{\frac{\sum_{j=1}^{n}(CPUE_j - \hat{CPUE}_j)^2}{n}},$$

where CPUE and $\hat{CPUE}$ are observed and predicted catch per unit of effort, respectively, and n is the number of years.

The distribution of the biomass of the stock in 1996–97 is summarized in Figure 8. There was more than a 70% chance that the biomass of the stock ranged between 1000 to 1750 t. The probabilities of short-term overharvest (i.e. exceeding the selected biological reference points) were calculated for different levels of catch in 1996–97 on the basis of the distribution estimated for the biomass of the stock in 1996–97 (Fig. 9). For example, the TAC of 100 t would have a 30% chance of exceeding the reference point f_{MSY}, and a 40% chance of exceeding $f_{0.1}$ (Fig. 9).

Discussion

The model used in this study is one of the simplest models commonly used in fish stock assessment (Hilborn and Walters, 1992). An essential assumption of this model, as with similar models, is that the relationship between CPUE and the biomass of the stock remains constant over time. Because of the use of the robust estimator, this assumption becomes the following: the proportional relationship between the

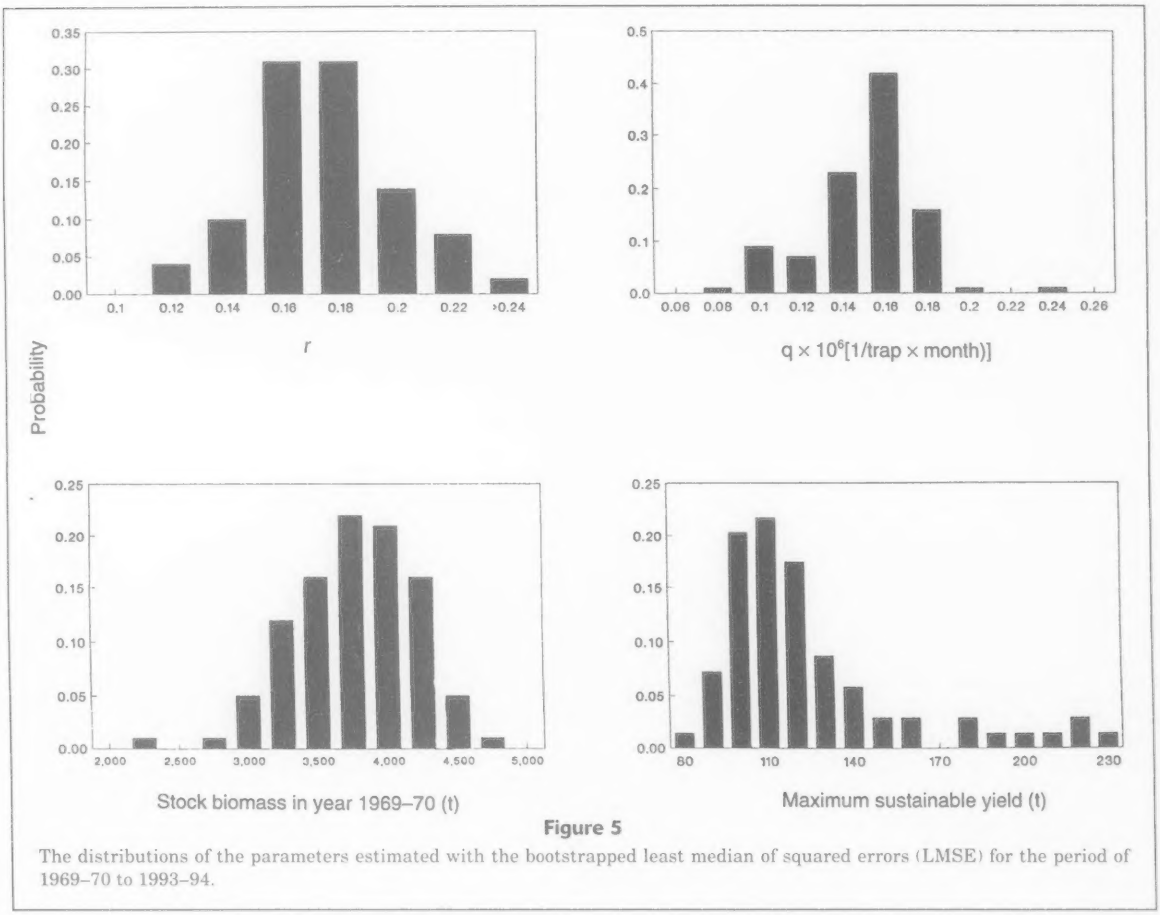

Figure 5

The distributions of the parameters estimated with the bootstrapped least median of squared errors (LMSE) for the period of 1969–70 to 1993–94.

stock biomass and CPUE is the same for the majority of years.

Compared with traditional least-squares estimation methods, the LMSE method tends to fit the model to the majority of the data, and its estimates of parameters are not affected by atypical data observed in a few years (Chen et al., 1994). Thus, if atypical observations arise, parameter estimation with the LMSE will not be affected greatly. Because the LMSE is not sensitive to atypical data, these data tend to be far from the LMSE-estimated CPUEs (Figs. 2 and 3) and thus are readily detected. However, it is important to determine why an observed CPUE is far from the predicted CPUE. Such a practice requires extensive background information on the fishery. Apart from exceptionally large observation errors, atypical observations may arise from unusual environmental conditions and substantial changes in fishing methods and locations. The nature of atypical observations resulting from unusual environmental conditions differs from those resulting from unusual observation errors. These atypical data should be considered separately from those observed under normal conditions in the stock assessment process because such unusual conditions last only for a short period of time in the development of the fishery (Chen et al., 1994). For example, the observed CPUE in 1971–72 was much higher than the LMSE-estimated CPUE (Fig. 4). This might result from the fishery being expanded in that year to include aggregations of lobsters on the previously unexploited slopes of the continental shelf. This would result in a high q for that year. Clearly, such a high level of CPUE cannot be sustained for long and should not be interpreted as an indicator of large stock biomass for that year. CPUEs observed from years 1917 to 1924 were much lower than the LMSE predicted (Fig. 2). This finding may be related to large observation errors in CPUEs. For this period, the number of fishing boats (other than trawlers or Dan-

ish seiners) that operated from lobster producing ports and in oceanic waters was used as an index of fishing effort for the lobster fishery. This was done because it was impossible to distinguish between vessels that were used for fishing lobsters and vessels that were used for fishing other species in the same area (Montgomery, 1995). During this period, annual landings of lobsters were probably under-reported because only lobsters sold at the main market centers were recorded. Such an over-estimation of efforts and under-estimation of catches would lead to under-estimation of CPUE for this period of time. It should be realized, however, that the above reasons for the large deviation of observed data from model estimates remain a working hypothesis.

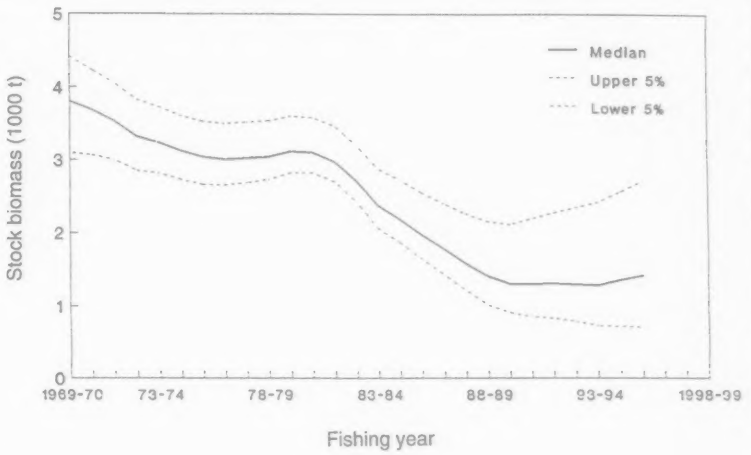

Figure 6

The median and 90% confidence intervals of stock biomass predicted with the bootstrapped LMSE method for the period of 1969–70 to 1995–96.

Outliers can be identified in linear regression analyses by using criteria developed by Rousseeuw and Leroy (1987). However, the criteria developed through extensive simulations based on a linear regression model cannot be used in nonlinear regression analysis. An extensive simulation study is needed to develop suitable criteria to identify outliers in nonlinear regression analyses. Before this can be done, the LMSE-based reweighted least squares, which has been shown to behave better than the least median of squares in linear regression analyses (Chen et al., 1994; Chen and Paloheimo, 1995), cannot be used in nonlinear regression analyses.

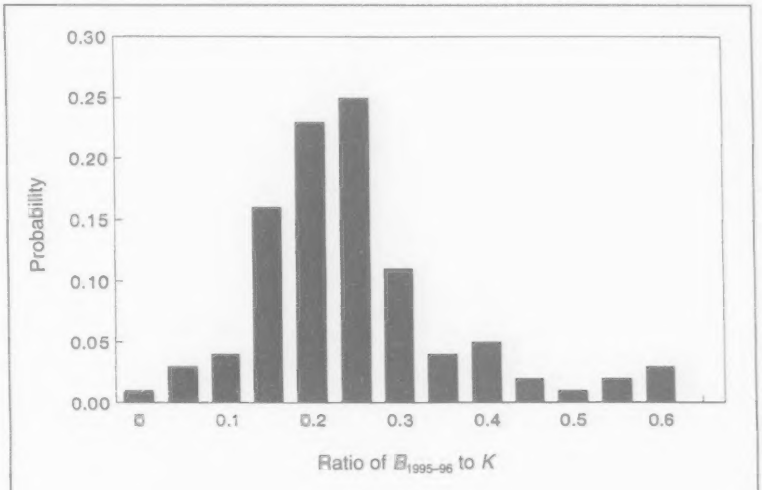

Figure 7

The distribution of the ratio between the biomass of the stock in 1995–96 ($B_{1995-96}$) and the biomass of the virgin stock (K) estimated with the bootstrapped LMSE method.

The results presented in our paper were based on catch data adjusted by using one set of adjustment coefficients. To test the sensitivity of the results to the adjustment coefficients, we also used two other sets of adjustment coefficients in the analysis (Table 4). These two sets of coefficients have more extreme values than the one presented in Table 1. The detailed results for these two sets of data were reported in Montgomery and Chen (1996). We plotted the stock biomass estimated with these three sets of data (Fig. 10). Although there are differences, they are rather small considering the large differences in adjustment coefficients. This may indicate that the results presented in this paper tend not to be sensitive to small changes in catch adjustment coefficients used in period II.

It is clear that the size of the lobster stock off New South Wales was low, with respect to its virgin biomass, as was the 75% confidence. Recent stock biomass (i.e. in 1995–96) has been between 15% and slightly over 30% of the virgin biomass. However, it seems that the decline in the biomass of the stock has stopped in recent years, and that the stock is perhaps in a period of recovery.

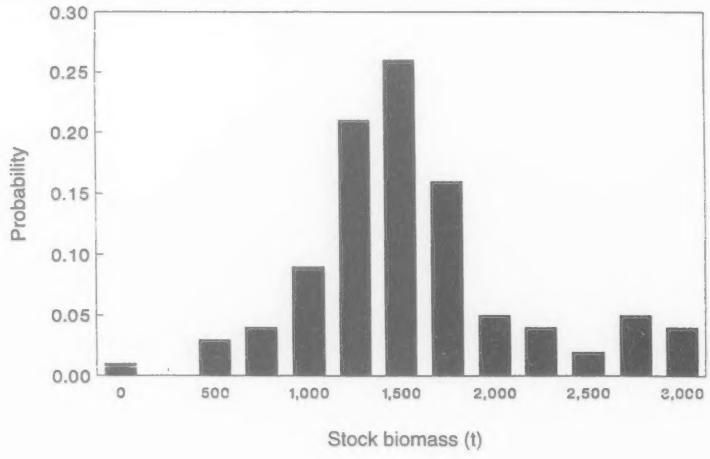

Figure 8

The distribution of stock biomass in 1996–97 estimated with the bootstrapped LMSE method.

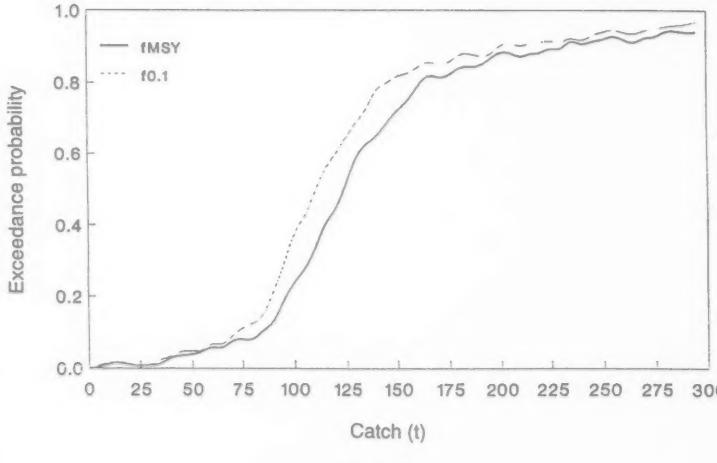

Figure 9

Probability of short-term overharvest (i.e. exceeding the selected reference points $f_{0.1}$ and f_{MSY}) for fishing year 1996–97.

Data observed in the two periods of time were modeled separately in our study. An alternative, perhaps better approach is to combine these two time periods with information on catches landed within the intervening period. This approach will be used in the next stock assessment when good estimates of catches from 1939 to 1968–69 become available.

Because the data were limited, the choice of models that can be used to describe the dynamics of lobster stock in NSW is also limited. Two disadvantages of using the simple production models are 1) an inadequate representation of the fishery dynamics may result in large biases in estimates of parameters and biomasses, and 2) extra assumptions are needed about fisheries (e.g. CPUE is a good indicator of stock abundance). However, these simple models also have their advantages. If the model fails, this failure can be seen easily. Because of the simple mathematical structure and lack of constraints in the parameter estimation, estimates of parameters may not necessarily be biologically reasonable (e.g. as negative values), an indication of the failure of models or data (Hilborn and Walters, 1992). It is now fashionable to mimic biological and fisheries realism by setting up a model that is mathematically and statistically complicated. Although advantages are obvious, disadvantages associated with this type of models may not always be realized. In addition to the requirement of extra input data, such models tend to have some undesirable attributes in the estimation of parameters, such as overfitting and high correlations among estimates of parameters. Incorporation of different biological and fisheries processes (e.g. fishing and recruitment processes) into one model for parameter estimation can also create some

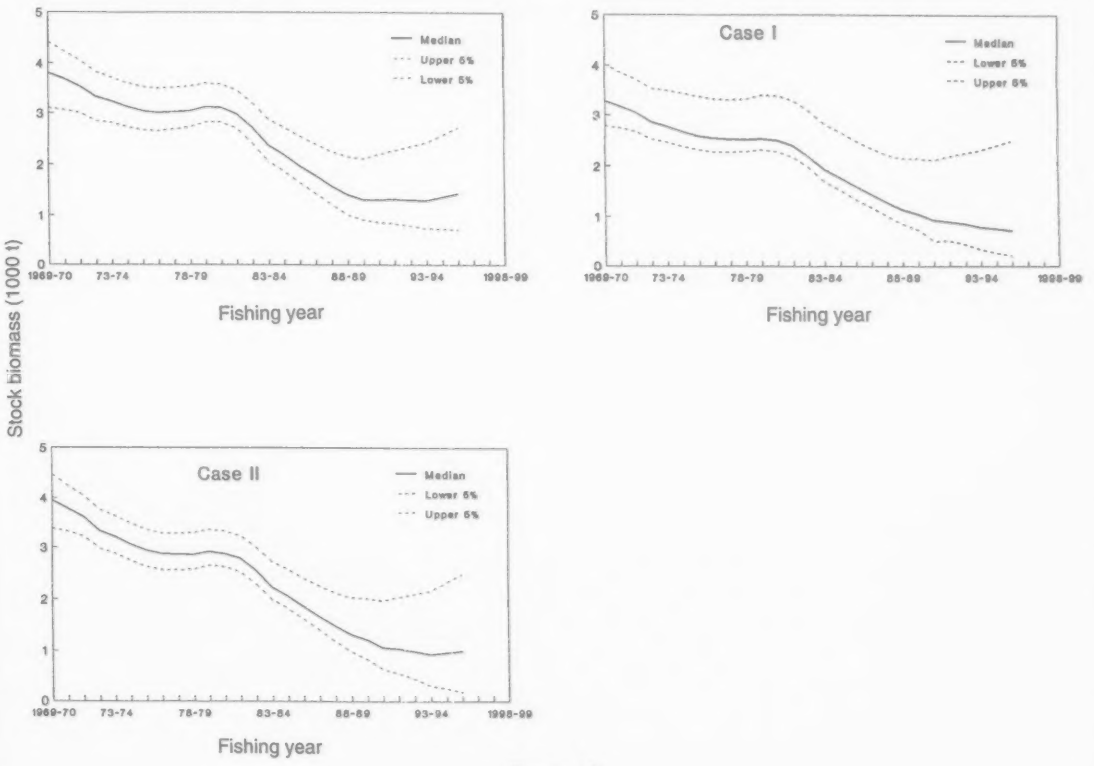

Figure 10

The predicted median and 90% confidence intervals of stock biomass for three sets of adjustment coefficients for the period of 1969–70 to 1995–96.

artificial links among parameters (e.g. between catchability coefficient and recruitment). A large number of built-in constraints (e.g. parameter A must have a value between A_1 and A_2) are often required to facilitate parameter estimation for such a model. This may artificially result in parameters having biologically reasonable estimates, even if the model fails. Such a feature also encourages the indiscriminate and uncritical use of stock assessment models, which leads to the misinterpretation of results. The extra biological or fisheries information (e.g. size structure, recruitment and spatial distribution) often incorporated into a dynamic model will certainly increase the accuracy and reliability in the estimation of parameters if the information is accurate. However, in practice, extra information is likely to be subject to large errors. In this case, a complicated model assimilating extra information will probably fail because its validation requires that each piece of information be true (Xiao[2]).

It is well known that the current biomass for a decreasing stock is often over-estimated when production models are used in assessment with the least squares method (e.g. Schnute, 1989; Hilborn and

Table 4

Coefficients used to test the sensitivity of the stock assessment to adjustment coefficients used to adjust reported catch data in the period from 1969–70 to 1993–94.

	Adjustment coefficient	
Year	Case I	Case II
1969–70 to 1979–80	0.4	0.6
1980–81 to 1989–90	0.6	0.7
1990–91 to 1991–92	0.3	0.5
1992–93 to 1993–94	0.1	0.2

[2] Xiao, Y. 1997. A theoretical consideration of subtleties in, and problems with, use of production models. Commonwealth Scientific and Industrial Research Organization (CSIRO) Marine Laboratory, Hobart, Australia. Unpubl. manuscript.

Walters, 1992; Polacheck et al., 1993; Chen and Andrew, 1998). In our study, when the maximum likelihood (ML) method was used, the r_I, q_I, and K_I had values of 0.041, 0.40×10^{-6} (per vessel), and 8,667 t, respectively. These are 20%, 23%, and 270% of the LMSE-estimated parameters, and 26%, 33%, and 213% of the median values of the bootstrapped LMSE estimates. According to the ML method, the eastern rock lobster stock had a large biomass with a low productivity rate. In contrast, the LMSE method predicted a smaller stock with a relatively high productivity rate. This difference arises from different methods used to fit the model to CPUE data. The ML was heavily influenced by the CPUEs observed from 1916 through 1924, whereas the LMSE virtually ignored these observations and tended to follow closely the CPUE in the majority of years (Fig. 11). Because of the high likelihood of under-estimation of CPUEs from 1916 through 1924, the LMSE method is probably more suitable. The estimates of r_{II}, q_{II}, and $B_{1969-70}$ by the ML method were 0.17, 0.13×10^{-6} (per trap-month) and 7174 t, differing from those estimated with the LMSE and bootstrapped LMSE methods (Table 3). This difference may result from different weightings of data for years 1971–72 and 1974–75. Fitting the model with the LMSE method virtually ignored the data observed in these years, which had much higher CPUEs than other years. However, fitting with the ML method was heavily influenced by these two years of high CPUEs (Fig. 11). Because of the patchy distribution of lobsters in their habitat and the expansion of fishing grounds out to the continental slope off the NSW coast during the early 1970s, it is very likely that these two years of exceptionally high CPUEs resulted from high fishing efficiency (i.e. high q values), which should not be taken as an indicator of high biomass.

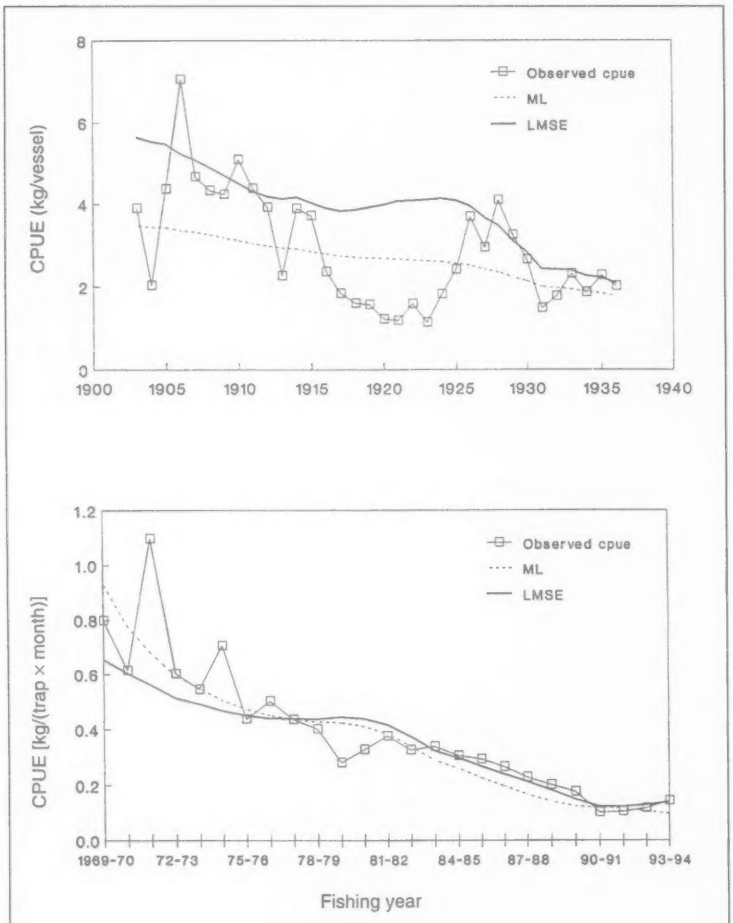

Figure 11

The predicted catch per unit of effort with the maximum likelihood (ML) and least median of squared errors (LMSE) methods for the period of 1903 to 1936 and the period of 1969–70 to 1993–94.

We suggest using the bootstrapped LMSE method as an alternative approach to fitting production models to catch-effort data. The results derived from such an analysis should be evaluated carefully with respect to the biology and ecology of the targeted fish species and with respect to how the catch-effort data were collected. Such an evaluation may shed some light on why some observations differ from the majority which the LMSE estimated line tends to follow. A comparison of results between robust and traditional least squares approaches may lead to a better understanding of the dynamics of the studied fish stock and identification of years in which atypical data are observed.

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Age and growth, dietary habits, and parasitism of the fourbeard rockling, *Enchelyopus cimbrius*, from the Gulf of Maine

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Abstract.–The fourbeard rockling, *Enchelyopus cimbrius*, is a small gadid fish found primarily over mud bottoms along the continental margins of the North Atlantic. This study defines the age classes of the fourbeard rockling from the Gulf of Maine, analyzes stomach contents, and characterizes the fish's metazoan parasite fauna. Age was determined from sectioned sagittal otoliths. Nine age classes were identified and compared with the Fraser-Lee back-calculation method. The rate of linear growth was constant throughout age classes. The diet of fourbeard rockling consisted primarily of bivalves, copepods, and decapods, in both number and frequency of occurrence indices. Prey composition in the diet changed with age. One-year-old fish preyed primarily upon copepods; bivalves were second in importance. The reverse was seen in 2–7 year old fish. Data on food habits suggest that the fourbeard rockling is a "grazer." Parasites of this species were one larval nematode, from the family Raphidascaridinae, one larval cestode, *Grillotia erinaceus*, and the two species of adult digenetic trematodes, *Genolinea laticauda* and *Gonocerca phycidis*. Prevalence and abundance data indicate that the parasitic fauna was dominated by Raphidascaridinae sp. and *G. erinaceus*.

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The fourbeard rockling, *Enchelyopus cimbrius* L., is a small gadid fish found primarily over soft mud or sand bottoms along the continental margins of the North Atlantic Ocean (Bigelow and Schroeder, 1953). This fish lives in burrows during daylight hours and forage at night (Keats and Steele, 1990). Although larval stages of *E. cimbrius* are well documented throughout its range (Battle, 1929; Demir et al., 1985), limited information exists about the age and growth of this species. This study estimates growth rates of *E. cimbrius* from the Gulf of Maine, analyses stomach contents, and characterizes the metazoan parasitic fauna.

Dietary studies for this species have been made at various localities in the eastern North Atlantic (Nagabhushanam, 1965; Wheeler, 1969; Mattson, 1981; Moller-Buchner et al., 1984; Tully and O Ceidigh, 1989), but little is known of the food habits for the western Atlantic, and there have been no dietary reports for *E. cimbrius* from the Gulf of Maine. Diets of *E. cimbrius* vary with location but have been found to consist primarily of polychaetes or crustaceans (Tyler, 1972; Langton and Bowman, 1980; Keats and Steele, 1990).

Records of parasitism of *E. cimbrius* are all apparently coincidental with parasite surveys. Reported parasites include a protozoan (Lom and Laird, 1969), a coccidian (Odense and Logan, 1976), an acanthocephalan (Linton, 1899), digenetic trematodes (Linton, 1899; Gibson and Bray, 1984; Brinkmann, 1988), and a nematode (Nagabhushanam, 1965). No survey of parasites to date has been specifically devoted to this host species.

Materials and methods

A collection of 727 fourbeard rocklings was obtained during the Gulf of Maine Northern Shrimp Survey GM 93-20, 2–13 August 1993. Collections were made during daylight hours at 41 randomly generated stations at depths ranging from 79 to 254 m aboard the NOAA RV *Gloria Michelle* equipped with a 4-seam modified commercial shrimp trawl with a 35-mm stretched mesh. In case of large hauls, a 1-kg random subsample was taken. An additional 36 fish, for stomach analyses, were collected from 6 stations at depths of 170–227 m during the GM 94-12 survey between 2 August and 3 August 1994 by using identical gear and methods.

Specimens collected during the GM 93-20 survey were frozen immediately at sea. To assess the effects of freezing on shrinkage, 218 fresh specimens were individually tagged, measured to the nearest mm for total length (TL), frozen, then remeasured after being thawed for 24 h. Fish were then weighed to the nearest g on a top loading balance and sexed. In addition, both

sagittal otoliths were extracted for ageing purposes and stored dry in coin envelopes.

Fish age classes were determined by counting presumed annual growth increments in otolith sections. For temperate-water fish, which generally exhibit seasonal growth patterns, one year of growth is defined by one opaque and one hyaline zone termed the "annulus" (Pentilla et al., 1988). Sagittal otoliths have been used for age determination in the majority of commercially important gadids (Andrade and Smith, 1988; Dery 1988; Pentilla, 1988) including *E. cimbrius* (Cohen et al, 1990). The assumption that increments were annual in *E. cimbrius* was based on the following: prolonged spawning in the Gulf of Maine (May–October) (Cohen et al, 1990), a pelagic stage (40.0–45.0 mm TL) spanning several months (Bigelow and Schroeder, 1953), time of year sample was taken (August), and presence of a prominent hyaline zone. The otolith of the smallest fish (95 mm TL) in the present study exhibits a prominent hyaline zone and this fish is assumed to have hatched in the previous year.

One otolith from each pair was embedded in a mixture of 1 part carbon powder and 4 parts paraffin wax, then sectioned dorsoventrally through the nucleus on an Isomet saw producing a section 203 µm thick. Sections were mounted on glass slides with Crystal Bond 509, polished with 3.0-µ and 0.5-µ metallurgic lapping film, etched for 6 minutes with 5% EDTA, and stained for 3 minutes with 0.1% toluidine blue. Otolith sections were viewed under a compound microscope at 40× by using transmitted light (Fig. 1). Etching with EDTA provided three-dimensional relief to the polished otolith surface, affording the greatest resolution and definition of the hyaline zones (Secor et al., 1992).

To reduce sample size for age determinations, the length-frequency distribution of *E. cimbrius* at station 40 was used to generate a rarefaction curve. Fifty-seven fish were aged by using both left and right sagittal otoliths during one trial under the following treatment effects: low-power dissecting microscope (LD); high-power zoom stereomicroscope (HS); and high-power zoom stereomicroscope after otoliths were etched with EDTA and stained with toluidine blue (EDTA). Nine fish were omitted from the analysis because of the inability to obtain either the left or the right otolith.

Individual variances of the six trials were plotted in groups of five to generate a rarefaction curve. The

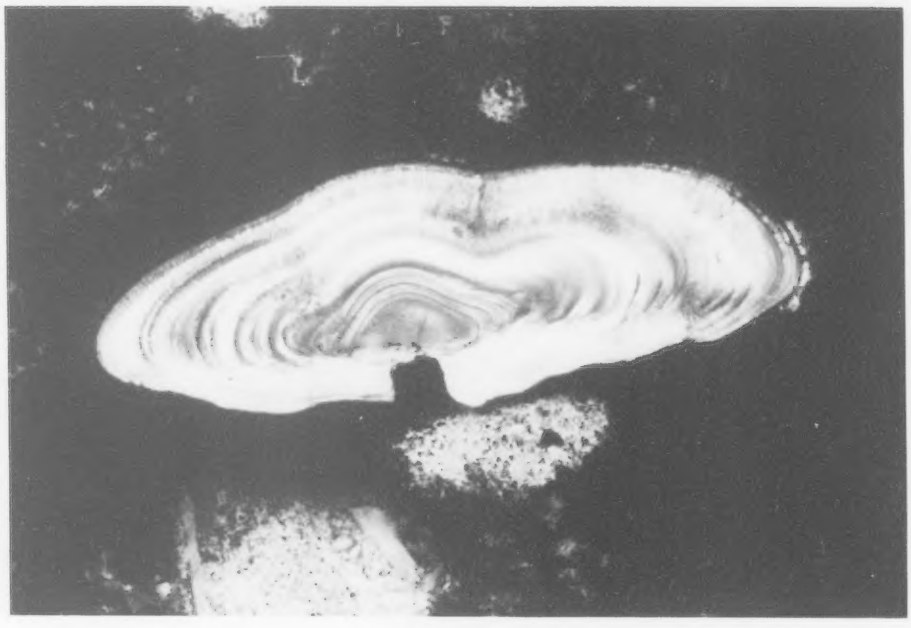

Figure 1

Transverse section of a sagittal otolith etched with 5% EDTA and stained with 0.01% toluidine blue photographed under a compound microscope at 40× by using transmitted light.

magnitude of the variance was stabilized at 30 fish per age class, yielding approximately 270 specimens to be aged. A length-based stratification was developed to avoid underrepresentation of the least abundant fish located at the extremes (Fournier, 1983). After removing the 77 lower (95–129 mm TL) and 54 upper (250–328 mm TL) extremes, 150 rocklings between 130 and 249 mm TL were randomly selected, then added to the extremes, yielding a total subsample size of 281 fish.

Otoliths from 281 fourbeard rocklings were etched and stained, then aged with a compound microscope at a magnification of 40 by using transmitted light. After three complete trials, an ANOVA was run on the assigned age classes.

Assigned age classes were compared by using the Fraser-Lee back-calculation formula which assumes that the relationship between individual fish length and otolith length is maintained proportionally throughout the back-calculation (Carlander, 1981)

It is defined as

$$L_i = a + OD_i(L_c - a/OR),$$

Where L_i = estimated total length (TL) when otolith has formed annulus i;
a = intercept of the (TL):otolith length (OL) regression determined from the sample;
OD_i = otolith distance from the nucleus to annulus i;
OR = otolith radius measured form the nucleus to the edge of the anterior rostrum; and
L_c = TL at capture.

Lengths at assigned ages were compared to back-calculated lengths at ages by means of correlation analysis. Total length back-calculation measurements were used to construct a length-frequency distribution to further corroborate ages assigned to length classes by otolith analysis. A Kolmogorov-Smirnoff test was used to test for differences between the observed and back-calculated length-frequency distributions.

Specimens from the GM 94-12 survey were labeled according to station, cut lengthwise along the abdomen, and preserved in 10% formalin. Stomachs were removed and their contents, after identification, summarized by using both numerical and frequency of occurrence indices. These analyses were further divided into two length categories: 1-year-old (105–121 mm TL) and 2–7 year old (119–271 mm TL) fish, on the basis of assigned age-class information. The size range of the first year class was calculated by using ±1 standard deviation from the mean. The second category, 2–7 year old fish, was calculated by using the –1 deviation of the mean size of the age-2 year class and the +1 deviation of the age-7 year class. Fish (n=1) that fitted within the size limits of these two age groups were placed in the category with the smallest difference between mean age-class length and length of the fish.

In addition to the 36 stomach samples from the GM 94-12 survey, a sample of 112 frozen fish from the GM 93-20 survey was obtained to inspect for occurrence of parasitism. Each gastrointestinal tract was removed and cut into its component parts, then sliced lengthwise to allow for inspection with a dissecting microscope. Nematodes were labeled according to the location of infection, preserved in 70% ethanol, then transferred to 70% ethanol and 5% glycerine.

Trypanorhynch blastocysts and digenetic trematodes were preserved and stored in 10% buffered formalin. Trypanorhynchs were removed from their blastocysts, transferred to 70% ethanol, and stained overnight in Mayer's paracarmine diluted 1:9 in 70% ethanol. Specimens were destained in 0.1 HCl in 70% ethanol until internal organs were visible, neutralized with 70% sodium bicarbonate for 20 minutes, then dehydrated in a graded ethanol series prior to clearing in methyl salicylate. Digenetic trematodes were similarly prepared. Each specimen was mounted on a glass slide in Canada balsam with slides stored flat until the mounting medium had hardened, when they were viewed under a dissecting scope for identification.

Helminth data were summarized by using prevalence, abundance, and intensity indicies. Prevalence (%P) is defined as the number of infected individuals divided by the number of individuals examined multiplied by 100, abundance (A) as the mean number of parasite species per host examined, and intensity range (I range) as the number of parasite species in each infected host (Margolis et al., 1982). Helminth data were further divided into nine length-class categories with ±1 standard deviation from the mean of each age class. Again, fish (n=3) that fitted within the limits of two age classes were treated in the same manner as in the food habits analysis. Splitting the data into length-class categories provided a better indication of the representative parasites in a respective year class than did dividing the data arbitrarily.

Results

Age and growth

The length-frequency distribution of *E. cimbrius* (n=727) sampled during the GM 93-20 survey ranged

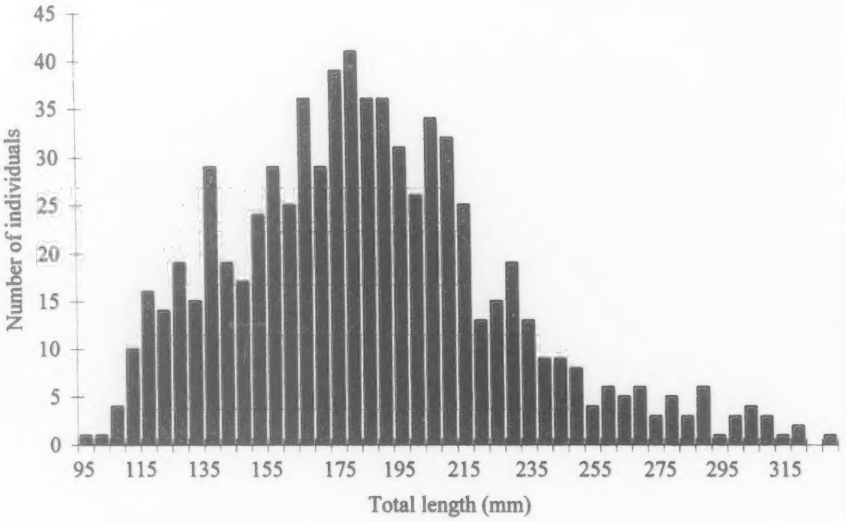

Figure 2

Length-frequency distribution of *E. cimbrius* collected during the GM 93-20 survey between 2 August and 13 August 1993 plotted in groups of 5 (e.g. 95=91–95). (n=727).

from 95 to 328 mm TL (Fig. 2). Shrinkage was not significant (P=0.2465), therefore, all total lengths reported in this study are from previously frozen fish.

None of the treatment effects (LD, HS, EDTA) employed on both otoliths from fish collected at station 40 was found to be significantly different (P=0.9488). The EDTA method was selected because it produced the highest r^2 value (r^2=0.9961) in a regression analysis. There was no significant difference between left and right otoliths (P=0.8934).

Nine age classes were identified (Table 1). An ANOVA was run on the assigned ages of the 281 rocklings. The three independent trials were not significantly different from one another (P=0.8028). There was a high correlation (P=0.984) between total length and age (Fig. 3). Because of the difficulty in interpreting annular growth or disagreement about age over the three independent readings, 28 out of 281 otoliths were discarded.

Linear growth was significantly different in males and females (P=0.0001) (Table 2). Nine male and eight female age classes were observed. To account for the sex differences in growth, the length frequency has been subdivided to show the distribution of male, female, and undetermined sexes (Fig. 4). Undetermined sexes were either immature or badly preserved.

There was a significant difference between the weights of males and females (P=0.0001). The average weight of all sexed specimens regardless of age showed that males weighed more than females (mean 26.5 ±19.3 and 24.5 ±24.2 g, respectively). Females were heavier at age than males for the first three year classes (Fig. 5). A scattergram of age versus total length (mm) and weight (g) is presented in Figure 6.

Regression analysis of TL vs. OL is defined by $y = 0.014x + 0.838$ where 0.838 is the intercept used to standardize the Fraser-Lee back-calculation equation. Back-calculated lengths at age (Table 3) and

Table 1

Age-class statistics based on observed otolith readings of *E. cimbrius* collected during the GM 93-20 survey between 2 August and 13 August 1993. (n=253).

		Total length (mm)		
Age class	n	Mean	Range	SD
1	37	112.6	95.0–127.0	8.1
2	52	127.4	115.0–149.0	8.5
3	24	157.3	142.0–178.0	8.8
4	38	180.5	155.0–207.0	12.4
5	35	204.3	189.0–226.0	9.2
6	16	240.7	223.0–268.0	13.8
7	26	258.5	228.0–282.0	12.8
8	13	283.6	272.0–297.0	6.8
9	12	307.7	293.0–328.0	9.9

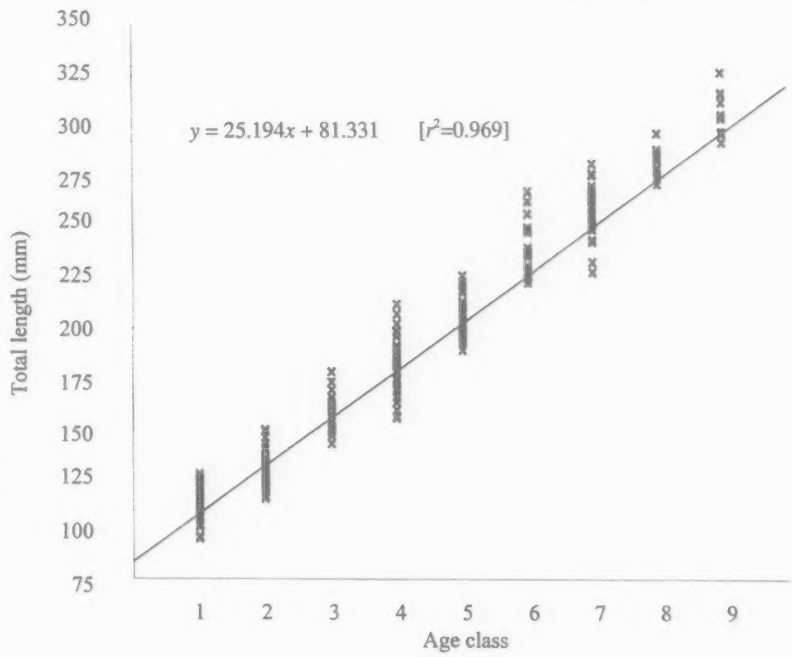

Figure 3

Regression of observed age-class data vs. total length (mm) of *E. cimbrius* collected during the GM 93-20 survey between 2 August and 13 August 1993. (n=253).

observed lengths at age were not significantly different (P=0.9608). The Kolmogorov-Smirnoff test revealed there was no significant difference between the back-calculated and observed length-frequency distributions (P=0.3124) (Fig. 7). In addition, back-calculated and observed lengths at ages were highly correlated (P=0.996).

Dietary habits

Stomach contents consisted primarily of mollusks and arthropods. Three specimens contained no food and were not included in the determination of numerical and frequency of occurrence indices. *Yoldia* sp. and calanoid copepods composed the majority of prey items in both number and frequency (Table 4). *Yoldia* sp. and calanoid copepods, combined with *Diastylis quadrispinosa*, *Crangon septemspinosa*, unidentified cumaceans and decapods, composed 91.6% of the prey items ingested. Frequency indices showed that the latter four prey items had similar frequencies.

Numerical indices show that copepods composed 71.2% of the diet of 1-year-old fish (Table 5). Bivalves were second in importance (19.2%), followed by cumaceans (5.4%), amphipods (2.7%), and decapods (1.4%). The importance of copepods decreased to

Table 2

Mean lengths of males, females, and immature or undetermined sexes per age class based on observed otolith readings. (n=253).

		Mean total length (mm)		
Age class	n	Male	Female	Immature or undetermined
1	37	116.7	113.3	110.7
2	52	130.6	125.7	125.8
3	24	158.0	155.8	160.3
4	38	180.0	181.2	—
5	35	204.0	204.5	—
6	16	239.4	242.8	—
7	26	257.9	257.5	277.0
8	13	281.8	287.0	286.0
9	12	307.7	—	—

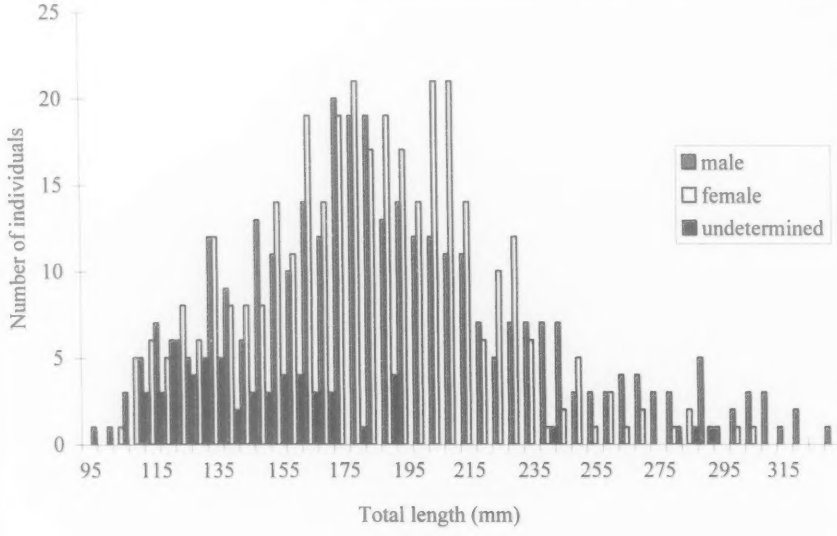

Figure 4

Length-frequency distribution of males, females, and undetermined sexes collected during the GM 93-20 survey between 2 August and 13 August 1993 plotted in groups of 5. (n=727).

28.7% and was replaced by bivalves (56.3%) in fish ranging from 2 to 7 years old (Table 5). Polychaetes (2.0%) and decapods (3.7%) were found only in the stomachs of older fish. Cumaceans made up a small percentage of the diet in both size ranges.

Bivalves (80.0%) and copepods (80.0%) were the most frequent items encountered in 1-year-olds, with cumaceans (40.0%) third in importance (Table 5). The frequency of bivalves (71.0%) in the diet of older fish was similar to that of 1-year-olds. Decapods and polychaetes were consumed in higher frequency in larger fish. Copepods were eaten in large numbers in both size categories but were taken less frequently by larger fish (12.9%).

Parasitism

Four parasite species were identified for the first time for this host. The nematodes were identified as all second- or third-stage and third- or fourth-stage larvae of the family Raphidascarinidae, probably *Hysterothylacium* sp. These identifications were based on the presence of a boring tooth, globular ventriculus, ventricular appendage, intestinal caecum, and excretory pore near the nerve ring. Raphidascarinidae sp., located mainly in the body cavity, were found to have the highest prevalence (23.0%) of all parasites surveyed (Table 6).

Table 3

Age-class statistics based on back-calculated lengths at age of *E. cimbrius* collected during the GM 93-20 survey between 2 August and 13 August 1993. (n=40).

	Total length (mm)		
Age class	Mean	Range	SD
1	102.3	86.0–118.0	8.1
2	127.7	116.0–140.0	6.8
3	153.8	140.0–174.0	8.0
4	183.1	167.0–202.0	9.5
5	212.9	191.0–231.0	10.0
6	235.5	223.0–260.0	9.6
7	257.1	244.0–270.0	8.2
8	280.0	272.0–287.0	6.2

Encysted plerocerci larvae were identified as *Grillotia erinaceus* Van Beneden, 1858 and were found in the body cavity, stomach, and intestine of 20.9% of the fish examined.

The two species of digenetic trematodes, found in the stomachs of *E. cimbrius* collected during the GM 94-12 survey, were identified as *Genolinea laticauda* Manter, 1925 and *Gonocerca phycidis* Manter, 1925. Body length dimensions of two specimens of *G.*

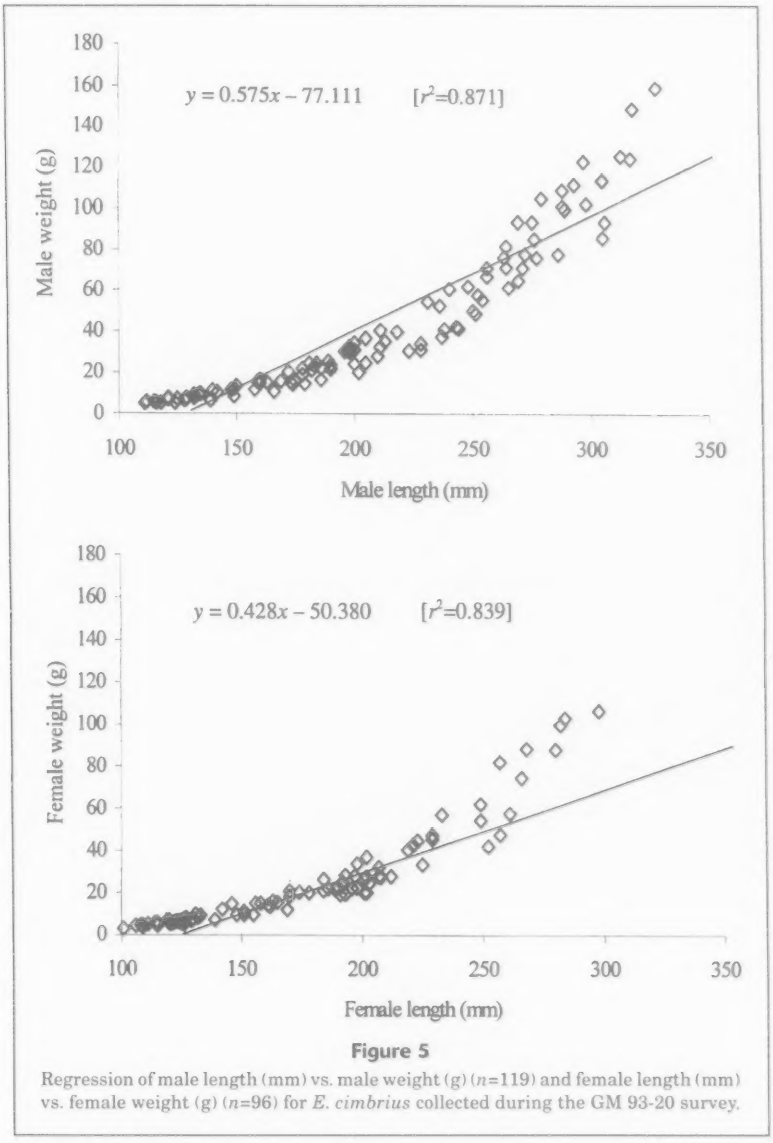

Figure 5

Regression of male length (mm) vs. male weight (g) (n=119) and female length (mm) vs. female weight (g) (n=96) for *E. cimbrius* collected during the GM 93-20 survey.

laticauda and *G. phycidis* ranged from 1.26 to 1.34 mm and from 1.38 to 1.76 mm, respectively. Both digenetic trematodes were found in low prevalence (4.7% and 1.4%, respectively) (Table 6).

The prevalence of infection of Raphidascarinidae sp. steadily increased from 8.3% in 1-year-olds to 100.0% in 9-year-olds (Table 7). The prevalence of *G. erinaceus* fluctuated but generally increased with fish age. There was an increase in infection from 9.1% to 20.0% and 25.0%, respectively by Raphidascarinidae sp. and *G. erinaceus* in 2- and 3-year-old fish. Infection by *G. laticauda* and *G. phycidis* was minimal in all size classes. All helminths in all year classes were found in low abundance.

Discussion

Age and growth

The age distribution of the sample comprised primarily of 3-, 4-, and 5-year-old *E. cimbrius*, with a maximum age of 9. The maximum age attained by this species in the Gulf of Maine is similar to that

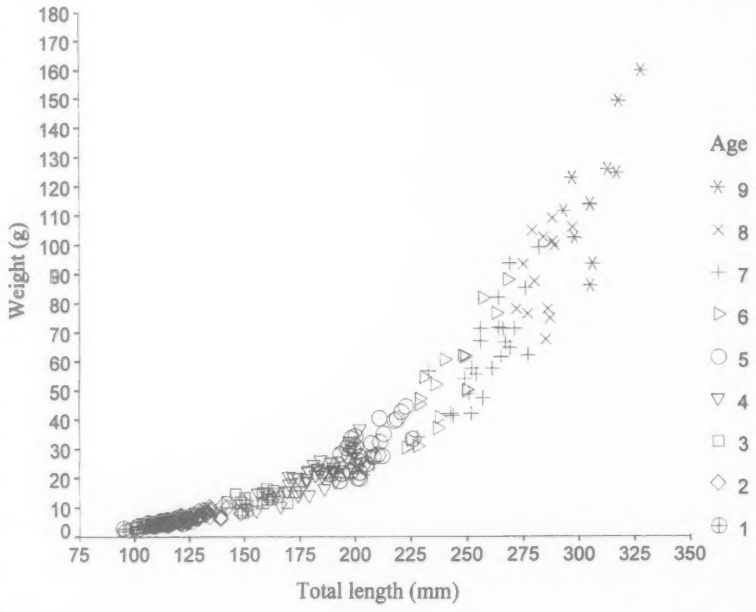

Figure 6

Scattergram of age vs. total length (mm) and weight (g) for *E. cimbrius* collected during the GM 93-20 survey. (n=241).

reported from the western and eastern Atlantic (Cohen et al., 1990). Age classes discerned in this study also agree well with those documented by Cohen et al. (1990) for the eastern Atlantic. Age classes for the eastern Atlantic are defined as follows: 3 years at 150 mm total length (TL), 5 years at 200 mm TL, 7 years at 250 mm TL, and 9 years at 290 mm TL (Cohen et al., 1990). The maximum length of *E. cimbrius* from this study (328 mm TL) again is similar to the maximum length recorded in the western Atlantic (305 mm TL) by Cohen et al. (1990).

The Kolmogorov-Smirnoff test showed no significant difference between length-frequency distributions of observed total lengths and back-calculated lengths derived from otolith increment data. This finding further corroborates that presumed annuli in sagittal otoliths were formed at regular time intervals and can be used to assign ages to length classes.

In aging studies, it is a common technique to compare assigned ages to length-frequency modes to confirm age classes (Campana and Jones, 1992). This was not attempted because of substantial overlap in the length-frequency modes of *E. cimbrius*. Length-frequency modes with substantial overlap have proven to be unreliable as predictors of component age groups because of several factors: the number of modes may be less than the number of components, modes may be obscured or indistinct, or false modes may be generated (Beamish and McFarlane, 1987). Fourbeard rocklings spawn from May to October (Battle, 1930; Cohen et al., 1990) and overlap in the length-frequency modes is likely due to this prolonged spawning season.

After the first year, the age-length relationship of fourbeard rocklings was linear. The young grew to an average of 113 mm during the first year, and, on average, grew 24 mm per year to age 9. The relative large size and narrow size range of one-year-old fish may be attributed to the under-representation of smaller fish in the sample size. Fast early growth, like that of *E. cimbrius*, is exhibited by most gadids, and is particularly evident in red hake, *Urophycis chuss*, and white hake, *U. tenuis*. This type of growth is probably advantageous to *U. chuss* and *U. tenuis* and to other small demersal marine fishes that enter habitats dominated by larger individuals (Markle et al., 1982). Arctic cod, *Boreogadus saida*, from Labrador also exhibits growth rates similar to that of *E. cimbrius*. After reaching approximately 90 mm in their first year, *B. saida* average roughly 40 mm per year until age 5; they rarely live beyond age 6 (Lear, 1983).

Table 4

Relative importance of prey items of *E. cimbrius* according to numerical and frequency of occurrence indices. (n=36).

Prey taxon	No.	%No.	Frequency	%Frequency
Phylum Mollusca				
Class Bivalvia	183	49.1	26	72.2
Order Protobranchia	183	49.1	26	72.2
Family Nuculanidae				
Yoldia sp.	183	49.1	26	72.2
Phylum Annelida				
Class Polychaeta	6	1.6	6	16.7
Family Phyllodocidae				
Unidentified Phyllodocidae	1	0.3	1	2.8
Paranaitis sp.	2	0.5	2	5.6
Family Nereidae				
Nereis sp.	1	0.3	1	2.8
Unidentified Polychaeta	2	0.5	2	5.6
Phylum Arthropoda				
Subphylum Mandibulata				
Class Crustacea	172	46.1	36	100.0
Order Copepoda	138	36.9	8	22.2
Suborder Calanoida	138	36.9	8	22.2
Subclass Malacostraca				
Series Eumalacostraca				
Superorder Peracarida				
Order Cumacea	13	3.5	9	25.0
Eudorella truncata	1	0.3	1	2.8
Diastylis quadrispinosa	7	1.9	4	11.1
Unidentified Cumacea	5	1.3	4	11.1
Order Isopoda	2	0.5	2	5.6
Unidentified Isopoda	2	0.5	2	14.0
Order Amphipoda	5	1.6	5	13.9
Family Hyperiidea				
Unidentified Hyperiidea	3	0.8	2	5.6
Family Calliopidae				
Calliopius laeviusculus	1	0.3	1	2.8
Family Gammaridae				
Unidentified Gammaridae	2	0.5	2	5.6
Order Mysidacea	1	0.3	1	2.8
Mysidopsis bigelowi	1	0.3	1	2.8
Order Decapoda	12	3.2	11	30.6
Infraorder Caridea				
Family Crangonidae				
Crangon septemspinosa	5	1.3	4	11.1
Family Pandalidae				
Unidentified Pandalidae	1	0.3	1	2.8
Unidentified Decapoda	4	1.1	4	11.1
Infraorder Brachyura				
Unidentified Brachyura	2	0.5	2	5.6
Animal remains	11	2.9	10	27.8
Unidentified vertebrates	1	0.3	1	2.8
Number examined	36			
Number empty	3			

Total length is the most appropriate parameter to set limits around an age class for *E. cimbrius*. For example, a fish with a total length of 165 mm would be approximately 3 or 4 years old. If the weight of this same fish, approximately 15 g, was used to estimate age, the range of this estimated age would increase from 2 to 5 years. Conversely, weight appears to be a better measure of absolute growth than total

Table 5

Relative importance of prey items of 1-year-old (105–121 mm TL) (n=5) and 2–7 year old (119–271 mm TL) (n=31) *E. cimbrius* based on numerical and frequency of occurrence indices.

	105–121 mm TL				119–271 mm TL			
Prey taxon	No.	%No.	Freq.	%Freq.	No.	%No.	Freq.	%Freq.
Phylum Mollusca								
Class Bivalvia	14	19.2	4	80.0	169	56.3	22	71.0
Order Protobranchia	14	19.2	4	80.0	169	56.3	22	71.0
Family Nuculanidae								
Yoldia sp.	14	19.2	4	80.0	169	56.3	22	71.0
Phylum Annelida								
Class Polychaeta	0	0.0	0	0.0	6	2.0	6	19.4
Family Phyllodocidae								
Unidentified Phyllodocidae	0		0		1	0.3	1	3.2
Paranaitis sp.	0		0		2	0.7	2	6.5
Family Nereidae								
Nereis sp.	0		0		1	0.3	1	3.2
Unidentified Polychaeta	0		0		2	0.7	2	6.5
Phylum Arthropoda								
Subphylum Mandibulata								
Class Crustacea	59	80.7	8	160.0	113	37.7	28	90.3
Order Copepoda	52	71.2	4	80.0	86	28.7	4	12.9
Suborder Calanoida	52	71.2	4	80.0	86	28.7	4	12.9
Subclass Malacostraca								
Series Eumalacostraca								
Superorder Peracarida								
Order Cumacea	4	5.4	2	40.0	9	3.0	7	22.6
Eudorella truncata	0		0		1	0.3	1	3.2
Diastylis quadrispinosa	2	2.7	1	20.0	5	1.7	3	9.7
Unidentified Cumacea	2	2.7	1	20.0	3	1.0	3	9.7
Order Isopoda	0	0.0	0	0.0	2	0.7	2	6.5
Unidentified Isopoda	0		0		2	0.7	2	6.5
Order Amphipoda	2	2.7	1	20.0	4	1.3	4	12.9
Family Hyperiidea								
Unidentified Hyperiidea	2	2.7	1	20.0	1	0.3	1	3.2
Family Calliopidae								
Calliopius laeviusculus	0		0		1	0.3	1	3.2
Family Gammaridae								
Unidentified Gammaridae	0		0		2	0.7	2	6.5
Order Mysidacea	0	0.0	0	0.0	1	0.3	1	3.2
Mysidopsis bigelowi	0		0		1	0.3	1	3.2
Order Decapoda	1	1.4	1	20.0	11	3.7	10	32.3
Infraorder Caridea								
Family Crangonidae								
Crangon septemspinosa	0		0		5	1.7	4	12.9
Family Pandalidae								
Unidentified Pandalidae	0		0		1	0.3	1	3.2
Unidentified Decapoda	1	1.4	1	20.0	3	1.0	3	9.7
Infraorder Brachyura								
Unidentified Brachyura	0		0		2	0.7	2	6.5
Animal remains	0	0.0	0	0.0	11	3.7	10	32.5
Unidentified vertebrate	0	0.0	0	0.0	1	0.3	1	3.2
Number examined	5				31			
Number empty	0				3			

length. The weight of fish between 300 mm and 325 mm TL ranged widely from 80 g to 160 g. After linear growth has slowed, fish still continue to gain weight.

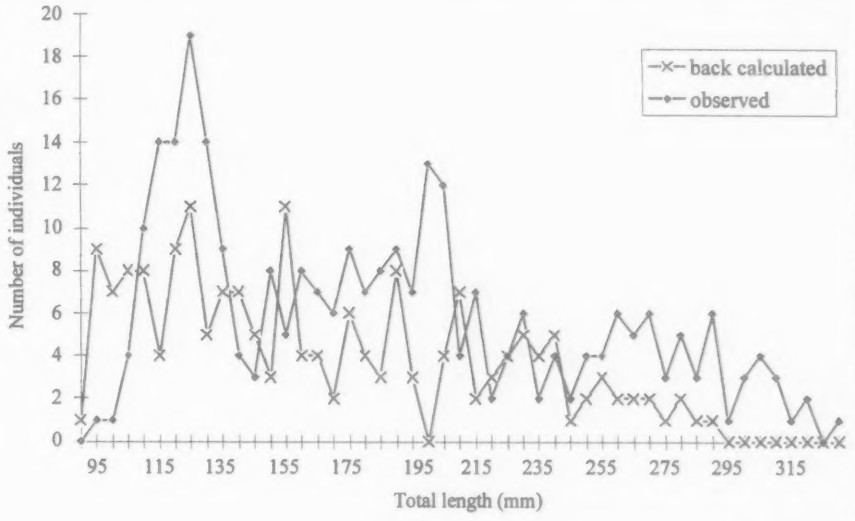

Figure 7

Length-frequency distribution of back-calculated lengths at age vs. observed lengths at age of *E. cimbrius* collected during the GM 93-20 survey between 2 August and 13 August 1993 plotted in groups of 5.

The dietary habits of *E. cimbrius* may contribute to its constant absolute growth. Fourbeard rocklings generally forage on small animals in large numbers instead of large animals in small numbers. Fishes that swim actively and forage for small organisms (i.e. "grazers") generally have a higher unit of energy expenditure per unit of energy input than do fishes that are lie-and-wait predators on large organisms. In addition, preference for cold temperatures may explain further why *E. cimbrius* exhibits constant linear growth. I speculate that *E. cimbrius* uses its energy to forage; energy that would otherwise have contributed to absolute growth.

Table 6

Prevalence (P), abundance (A), standard error (SE), and intensity (I) of Raphidascaridinae sp., *Grillotia erinaceus*, *Genolinea laticauda*, and *Gonocerca phycidis* in *E. cimbrius* collected during the GM 93-20 and GM 94-12 surveys.

Parasite	*n*	P (%)	A ± SE	I range
Raphidascaridinae sp.	34	23.0	1.69 ± 1.24	1–32
Grillotia erinaceus	31	20.9	1.65 ± 0.25	1–8
Genolinea laticauda	7	4.7	4.33 ± 0.96	1–7
Gonocerca phycidis	1	1.4	2.00 ± 0.00	2

Dietary habits

Prey items of *E. cimbrius* surveyed in this study were predominately bivalves, particularly *Yoldia* sp., in both number and frequency. Calanoid copepods, although present in great numbers, were consumed by few individuals. The importance of copepods is replaced by bivalves, *Yoldia* sp., and polychaetes in the diet of larger fish (>119 mm TL). After their first year, fish shift from a diet dominated by planktonic copepods to a diet comprising infauna (bivalves and polychaetes).

Calanoid copepods composed the majority (71.2%) of the prey taken, with bivalves (although consumed in relatively high frequency (80.0%)) second in importance by number (19.2%) in 1-year-old fish. Juveniles in the present study exhibited feeding preferences for various calanoid copepods similar to those of pelagic larval gadids off the Isle of Man (Nagabhushanam, 1965.) This preference for planktonic organisms suggests that juveniles lead a less sedentary existence and feed more frequently in the water column than do adults. In addition, the selection for smaller prey is directly related to mouth size (Moyle and Cech, 1988).

On Georges Bank, fourbeard rocklings >100 mm TL consumed motile epifauna, particularly *Crangon septemspinosa* (46.3%), in the highest percentage by

Table 7

Prevalence of infection (P%) and abundance (A) of four species of helminths in age-class ranges from *E. cimbrius* collected during the GM 93-20 and GM 94-12 surveys. (n=148).

		Raphidascaridinae sp.		*G. erinaceus*		*G. laticauda*		*G. phycidis*	
Age class	n	P(%)	A	P(%)	A	P(%)	A	P(%)	A
1	12	8.3	0.1	16.7	0.2	0.0	0.0	0.0	0.0
2	11	9.1	0.5	9.1	0.2	9.1	0.2	9.1	0.2
3	20	20.0	0.3	25.0	0.3	0.0	0.0	0.0	0.0
4	51	21.6	1.3	17.6	0.2	5.9	0.2	0.0	0.0
5	27	26.0	2.3	14.8	0.4	3.7	0.2	0.0	0.0
6	15	26.7	1.9	20.0	0.4	6.7	0.5	0.0	0.0
7	8	37.5	1.5	37.5	0.4	0.0	0.0	0.0	0.0
8	2	50.0	1.0	100.0	1.5	0.0	0.0	0.0	0.0
9	2	100.0	2.5	100.0	2.5	0.0	0.0	0.0	0.0

weight followed by animal remains (30.1%) and infauna, primarily polychaetes (13.6%) (Langton and Bowman, 1980). Decapod crustaceans were not as important as these other groups to juvenile fish in the present study. Decapods appeared in number for the first time in 2- to 7-year-old fish. This can be explained by the preference for larger prey by older, larger fish.

In a Norwegian fjord, *E. cimbrius* between 70 and 300 mm TL preyed primarily on crustaceans, polychaetes, fish, bivalves and rarely on copepods (Mattson, 1981). In adult rocklings, high percentages of infauna, particularly polychaetes, have been reported from the North Sea (Moller-Buchner et al., 1984) and Passamaquoddy Bay, where the frequency was found to be correlated with an increase in fish size (Keats and Steel, 1990). The high frequency of infaunal organisms, predominantly bivalves, in the diet of 2- to 7-year-old fish in the present study exhibits a similar trend. This finding may be correlated with adults having a sedentary existence and remaining in close contact with the substrate (Bigelow and Schroeder, 1953; Cohen et al., 1990). This lifestyle, compounded with the fact that this species has well-developed stout barbels equipped with taste buds (Nagabhushanam, 1965), would enable larger fish to feed more effectively on epifauna and infauna.

E. cimbrius is best characterized as a euryphagous bottom-rover or "grazer." (Moyle and Cech, 1988). The size of the prey appears to be directly correlated with the size of the predator as seen in the change in diet from 1-year-old fish to those 2 to 7 years of age.

Parasitism

The parasite fauna of *E. cimbrius* consisted of three taxa and four species: Nematoda (1), Cestoda (1), and Trematoda (2). The prevalence (P%) and abundance (A) of a nematode from the subfamily Raphidascaridinae (probably *Hysterothylacium*) and a trypanorhynch cestode, *G. erinaceus*, appear to increase with fish age. The P% and A of both digenetic trematodes were low in all age classes.

The few helminths found were in low abundance. This is uncommon because other gadids are known to have abundant and diverse parasite faunas (Margolis and Arthur, 1979). The very low parasite diversity of *E. cimbrius* supports evidence of limited movements and benthic feeding preferences in its habitat.

All nematode specimens of the subfamily Raphidascaridinae were second- or third-stage and third- or fourth-stage larvae (Measures[1]). The presence of parasites in the same stage of development are indicative of a "grazer" (Dogiel, 1966) and provides additional support to characterize *E. cimbrius* as such. A similar trend is seen in *G. morhua*, where its mode of life, generalist feeding habits, and association with the bottom facilitate the infestation by *Raphidascaridinae* spp. (Dogiel et al., 1970).

The increase in prevalence of *Grillotia erinaceus* from 9.1% at 2 years to 25.0% at 3 years appears to be correlated with the an increase of arthropods in the diet. In the life cycle of *G. erinaceus*, the plerocercus larvae can be acquired by an intermediate teleost host through consumption of arthropods, mainly copepods, which have previously ingested the tapeworm eggs (Sakanari and Moser, 1985). It is not possible to draw any firm conclusions on this relationship because food habit data in this study did

[1] Measures, L. 1995. Maurice Lamontagne Institute, Fisheries and Oceans, Mont-Joli (Quebec), Canada G5H 3Z4. Personal commun.

not account for seasonal variation and because the sample size of 8- and 9-year-old fish was low.

The definitive hosts of adult trypanorhynchs are elasmobranchs, suggesting that fourbeard rocklings are consumed by elasmobranchs or act as paratenic hosts. It is likely that barndoor skate, *Raja laevis*, and thorny skate, *Raja radiata*, prey upon *E. cimbrius*. *Raja laevis* and *R. radiata* >700 mm TL forage primarily on fish that include hake, *Urophycis* spp., and whiting, *Merluccius* spp., and may also feed on cod and haddock (Bigelow and Schroeder, 1953; McEachran et al., 1976). Because both *Raja* spp. consume fishes with similar habits and are definitive hosts for *G. erinaceus* (Margolis and Arthur, 1979), it is probable that *R. laevis* and *R. radiata* prey upon *E. cimbrius*.

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Genetic identification of sharks in the U.S. Atlantic large coastal shark fishery*

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Abstract.–Nucleotide sequences of a 394–396 base pair fragment of mitochondrial (mt) DNA, including parts of the cytochrome *b* and threonine tRNA genes, were obtained for eleven species of carcharhiniform sharks important to the U.S. Atlantic large coastal shark fishery. Sequences were used to predict sizes of restriction fragments produced by 118 restriction enzymes with unique recognition sequences. Seven restriction enzymes were chosen that produce an array of species-specific fragments for the eleven species. Geographic variation was examined in several species by surveying specimens from geographically distant regions. Only one of the species, the spinner shark *(Carcharhinus brevipinna)*, exhibited geographic variation in mtDNA restriction fragments. The sandbar shark (*C. plumbeus*) exhibited sequence polymorphism that did not produce differences in restriction patterns of any of the seven enzymes. We detected numerous differences between observed restriction patterns in ten tiger sharks (*Galeocerdo cuvier*) and patterns predicted from a published sequence. We concluded that the published sequence is incorrect. Amplification of a single PCR product from a sample of meat, digestion of aliquots of the product with restriction enzymes, and sizing of fragments on agarose gels is an efficient method for distinguishing among these eleven carcharhiniform sharks. The method can be applied when only a small amount of tissue is available.

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The U.S. Atlantic large coastal shark fishery grew rapidly during the 1980s when commercial landings increased from 135 metric tons (t) in 1979 to a high of 7122 t in 1989 (NMFS, 1993). In 1993, a quota of 2750 t was established; in 1997 this quota was halved to 1375 t in order to rebuild depleted shark stocks. This fishery targets several species of sharks that are valued for fins (exported to Asia) and meat (sold domestically). Because of the slow growth rate, high age at maturity, and low fecundity of most shark species (Pratt and Casey, 1990), commercial shark fisheries typically collapse after a brief period unless strict conservation measures are implemented (Holden, 1974, 1977; Hoenig and Gruber, 1990). The 1993 shark fishery management plan divided exploited species into three categories: large coastal sharks, small coastal sharks, and pelagic sharks (NMFS, 1993). The category that grew most rapidly was the large coastal shark fishery, which is dominated by several species of requiem sharks and two species of hammerhead sharks.

Sound management of a multispecies fishery requires information on the vulnerability of each component of the fishery. Differences in life history characters, e.g. intrinsic growth rates, locations of nursery areas, or migration within or outside of the fished area, can result in different vulnerabilities to overfishing of exploited species. For example, Musick et al. (1993) reported a relative decline in the dusky shark (*Carcharhinus obscurus*) off Virginia during expansion of the large coastal shark fishery. Thus, it is important to estimate catches on a species-by-species basis and to implement species-specific management. In the event that regulations (e.g. moratoria or minimum size limits) are applied to individual species, enforcement will rely on identification of protected species within the catch. The manner in which sharks are processed at sea, however, makes it difficult to accurately identify species at landing. Sharks typically are headed, gutted, and finned (i.e. fins are removed), thus destroying morphological characters necessary for species identification. Although Castro (1993) recommended a suite of characters for identification of shark carcasses, the limited number of available morphological characters makes it difficult to distinguish among several species. Martin (1993) suggested that use of restriction-frag-

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ment differences in polymerase chain reaction (PCR) amplified DNA might provide a rapid and inexpensive means of identifying carcasses and fins. We develop this technique as a means of identifying the eleven most frequently landed carcharhiniform sharks in the U.S. east coast longline fishery.

Materials and methods

Tissues (heart, white muscle, or fin) from nine species of carcharhinid sharks and two species of sphyrnid sharks were obtained from commercial fishermen, sport tournaments, and research longlining cruises (Table 1). Tissues were either frozen in the field and stored at –80°C or preserved immediately in 10× Longmire's lysis buffer (0.1 M tris, 0.1 M Na_2EDTA, 0.01 M NaCl, 0.5% SDS, pH 8.0) at room temperature. Genomic DNA was isolated by first powdering tissue under liquid nitrogen with a prechilled mortar and pestle. Approximately 100 mg of powdered tissue were suspended in 500 µL STE buffer (0.1 M NaCl, 50 mM tris, 1 mM EDTA; pH 7.5) and lysed with 25 µL 20% SDS. Genomic DNA was extracted twice with phenol:chloroform:isoamyl alcohol (25:24:1) and twice with chloroform:isoamyl alcohol (24:1). DNA in aqueous phase was precipitated by adding 2.5 volumes of ice-cold absolute ethanol and 0.1 volumes of 3M NaOAC, stored at –20°C for at least two hours, centrifuged for 15 min at 4°C at maximum speed in a microcentrifuge, and rinsed with 70% ethanol.

PCR amplification for cycle sequencing or restriction-enzyme digestion was accomplished by using a suite of PCR primers. The "diagnostic" fragment used in digestions consisted of a single segment, 394–396 bp in length, that was amplified by using light-strand primer Cb3RL (CATATTAAACCCGAATGATAYTT) located within the 3' domain of the mitochondrially encoded cytochrome *b* (cyt *b*) gene and heavy-strand primer Cb6H (CTCCAGTCTTCGRCTTACAAG) located within the mitochondrially encoded threonine tRNA ($tRNA^{THR}$) gene (Martin and Palumbi, 1993). This fragment was sequenced through the primer sites by using additional primer sets within and outside the diagnostic fragment. PCR fragments were prepared for sequencing by using the Bio-Rad Prep-a-Gene DNA purification system that removes extraneous salts, primers, and small fragments of DNA prior to cycle sequencing. Dideoxy DNA sequencing was performed with the Promega *fmol* DNA sequencing system by using ^{32}P end-labeled primers. Cycle sequencing reactions consisted of a single two-minute denaturing process at 95°C, followed by thirty cycles of 1 min at 95°C, 30 sec at 64°C, and 30 sec at 72°C. Sequencing reactions were scored on 6% denaturing

Table 1

Sources of tissues or DNA sequences. EMBL/Genbank accession numbers identify sequences from Martin and Palumbi (1993).

Species	Acronym	Source of sequence	Source of specimen
Bignose shark (*Carcharhinus altimus*)	Cal-A	This study	Virginia, Atlantic Ocean
Blacktip shark (*C. limbatus*)	Cli-A	"	Virginia, Atlantic Ocean
Bull shark (*C. leucas*)	Cle-A	"	Florida, Gulf of Mexico
Dusky shark (*C. obscurus*)	Cob-A	"	Virginia, Atlantic Ocean
Sandbar shark (A) (*C. plumbeus*)	Cpl-A	GenBank L08032	Hawaii, Pacific Ocean
Sandbar shark (B)	Cpl-B	This study	Florida, Gulf of Mexico
Sandbar shark (C)	Cpl-C	"	Hawaii, Pacific Ocean
Silky shark (*C. falciformis*)	Cfa-A	"	Hawaii, Pacific Ocean
Spinner shark (A) (*C. brevipinna*)	Cbr-A	"	Pacific Ocean, Australia
Spinner shark (B)	Cbr-B	"	Virginia, Atlantic Ocean
Lemon shark (*Negaprion brevirostris*)	Nbr-B	GenBank L08039	Florida, Atlantic Ocean
"Tiger shark" (A)[1] (*Galeocerdo cuvier*)	Gcu-A	GenBank L08034	Hawaii, Pacific Ocean
Tiger shark (B)	Gcu-A	This study GenBank AF004288	Florida, Gulf of Mexico
Great hammerhead (*Sphyrna mokarran*)	Smo-A	"	Florida, Gulf of Mexico
Scalloped hammerhead (*S. lewini*)	Sle-A	GenBank L08041	Hawaii, Pacific Ocean

[1] It was determined that this sequence was not tiger shark (see text).

polyacrylamide gels and examined by autoradiography. DNA sequences were read on an IBI gel reader and entered directly into computer text files. Sequences were confirmed by recording a minimum of two separate sequencing runs through each base. Sequences were aligned by using the ESEE software package (Cabot and Beckenback, 1989). Four cyt *b* sequences—those of sandbar (*C. plumbeus*), lemon (*Negaprion brevirostris*), tiger (*Galeocerdo cuvier*), and great hammerhead sharks (*Sphyrna mokarran*)—were downloaded from the EMBL/NCBI Genbank database (Martin and Palumbi, 1993). All other cyt *b* sequences and all $tRNA^{THR}$ sequences were acquired from our laboratory.

Sequences from each species between primers Cb3RL and Cb6H were concatenated with sequences of the primers to produce a single sequence for each of the eleven species (Table 2). Sequences were examined for predicted restriction sites with IBI MacVector software (IBI Mac Vector, 1991). One hundred eighteen restriction enzymes with unique recognition sequences were used in the search for restriction sites.

Amplified "diagnostic" fragments were prepared by amplifying genomic DNA at thirty cycles of 95°C for 1 min, 48 to 52°C for 30 sec, and 72°C for 30 sec. Amplified fragments were ethanol precipitated as above and reconstituted in water. Generally, one 100 µL PCR reaction produced enough diagnostic fragment for all seven restriction digestions. Fragments were digested by using manufacturer's buffers and specifications. Most restriction patterns were scored on 2% agarose gels run on 1X TAE. Fragments between 40 and 100 bp were scored on either vertical nondenaturing polyacrylamide gels or 2% nusieve 3:1 agarose gels. Fragments less that 40 bp were not scored, although loss of fragments as small as 24 bp could be inferred from mobility shifts in larger fragments. All gels were stained with ethidium bromide and examined under UV light (Sambrook et al., 1989).

Results

A single mtDNA fragment of 394–396 bp that contained the 3' end of cyt *b* and part of the $tRNA^{THR}$ gene was amplified in all species. Except for two hammerhead sharks, the fragment was 395 bp in length (Table 2). Cyt *b* sequences from all eleven species were identical in length and unambiguously aligned. In comparison with the other nine species, the scalloped hammerhead (*S. lewini*) possessed a single-base deletion in the $tRNA^{THR}$ sequence, and the great hammerhead possessed a single-base insertion in the $tRNA^{THR}$ sequence.

In bignose shark (*C. altimus*), three fragments of sizes 395 bp, 720 bp, and 1040 bp were produced repeatedly. The additional bands were more pronounced at lower (48°C) than higher (52°C) annealing temperatures. Further investigation with additional primers revealed that bignose shark possessed a much larger mitochondrial D-loop region than any other shark in the study. Amplification with a light-strand primer located within cyt *b* and a heavy-strand primer located within the 12S ribosomal RNA gene produced an approximately 1400-bp fragment in all species except bignose shark, where a single fragment of approximately 2000 bp was produced. We hypothesize that the Cb6H recognition site within the $tRNA^{THR}$ gene is duplicated twice within the D-loop of the bignose shark, resulting in a three-banded amplification product. Duplication of segments of flanking regions within the mitochondrial D-loop have been reported in other vertebrates (Broughton and Dowling, 1994, and citations within). To our knowledge, this is the first evidence of this phenomenon in elasmobranchs. To obtain the single product for sequencing and restricting, the 395-bp fragment was excised from an agarose gel and reamplified to produce sufficient amounts of the diagnostic fragment.

Of 118 restriction enzymes surveyed by MacVector software, 34 were predicted to have restriction sites within one or more of the eleven species. Seven restriction enzymes (*Alu*I, *Dde*I, *Fok*I, *Hae*III, *Hinc*II, *Hinf*I, and *Rsa*I) were chosen for screening because use of these seven enzymes allowed all eleven species to be distinguished (Table 3). The number of sharks whose mtDNA was subjected to restriction-enzyme digestion is given in Table 4. The initial screen of restriction sites was undertaken with only a single sequence from each species. Differences in predicted and observed restriction patterns in three species (sandbar, spinner, and tiger sharks) made it necessary to sequence additional animals in order to investigate whether differences were due to sequencing errors or intraspecific variation.

Observed restriction patterns in sandbar sharks from the Gulf of Mexico differed by restriction site from the pattern predicted from the published sequence of Martin and Palumbi (1993) for a sandbar shark (Cpl-A) from Hawaii (Martin[1]). Although we predicted that *Fok*I would not cut the sandbar shark fragment, *Fok*I digestion produced two fragments of 310 and 85 bp. We sequenced additional sandbar sharks from the Gulf of Mexico (Cpl-B) and from Hawaii (Cpl-C) and found that both sequences possessed the *Fok*I restriction site. Sequence of the speci-

[1] Martin, A. P. 1997. University of Nevada-Las Vegas, Las Vegas, NV 89154-4004. Personal commun.

Table 2

DNA Sequences used to predict restriction digests. Boxes surround primer sequences used in PCR amplification (A=adenine, C=cytosine, G=guanine, T=thymidine, Y=C or T). A vertical line is drawn between the end of the cytochrome *b* sequence and the beginning of the threonine tRNA sequence. See Table 1 for description of samples.

```
          5'  Cb3RL  ->

Cal-A     CATATTAAACCCGAATGATAYTT CTTATTTGCTTATGCAATCCTGCGCTCAATCCCTAATAAACTAGGAGGAGTCCTAGC
Cbr-A     ....................... ............C......T.A..............C.....................
Cbr-B     ....................... ............C......T.A..............C.....................
Cfa-A     ....................... ......C.....C......T.A........T.........................
Cle-A     ....................... ....................A...........C.........................
Cli-A     ....................... ......C..C...........A........T.........................
Cob-A     ....................... ..................TT.A...........C.......................
Cpl-A     ....................... ..........................................................
Cpl-B     ....................... ..........................................................
Cpl-C     ....................... ..........................................................
Gcu-A     ....................... .C.......C.........T.C..G...........C.....................
Gcu-B     ....................... ....................T.A..T..T.....C..................T.....
Nbr-A     ....................... .........C...........A.....T..T.....C.....................
Sle-A     ....................... .C....C..C.........T.A.....T..T.....C................T....
Smo-A     ....................... ......C..C.........T.A.....C..T.....C.....................

Cal-A     TCTCCTATTCTCTATCTTCATCCTTATATTGGTGCCCCTCCTCCACACCTCCAAACAACGAAGTACCATCTTCCGACCCA
Cbr-A     C..............T..T.....C.....A..C..T.........T.....................T..............
Cbr-B     C..............T..T.....C.....A..C..T.........T..........................................
Cfa-A     ........................C........T..T.............................C........T.......
Cle-A     C........T..C..T..T...........A..T..T.....................................................T.
Cli-A     ............C.....T...........AA.T..T..............T.............................T
Cob-A     C...........G.....T.....C.....A..T..T.............................C...G.............
Cpl-A     ..................T.....................................................................
Cpl-B     ..........................................................................................
Cpl-C     ..........................................................................................
Gcu-A     C........T.....TC.T...........A..T..T.....T..A.....T.....................................A.
Gcu-B     C..AG..........T........C...C.AA.T..T..T...........T...........C.G..C.........AAC
Nbr-A     C...........C..T........C...C.A..C.....T...........A.............T.............TC
Sle-A     C..TT.......A.....T.....C...C.A..T..A..A..T.....................A.............AC
Smo-A     ............C.....T.....C...C.A..C.TTTA...T........T.............A.............AC
```

continued

men from the Gulf of Mexico (Cpl-B) differed from that of the specimen from Hawaii (Cpl-C) by three base-pair substitutions. The sequence from the specimen from Hawaii (Cpl-C) differed from that of Martin and Palumbi (1993) by one base-pair (and which affected the *Fok*I restriction site). Whether the single base pair difference between our specimen from Hawaii and the one reported in Martin and Palumbi (1993) represents an uncommon polymorphism in sandbar sharks from the Pacific or an error in reading the original sequence cannot be determined. We examined restriction digestions from three sandbar sharks collected near Hawaii and all possessed the *Fok*I restriction site.

We also found a populational difference between spinner sharks (*C. brevipinna*) collected from the North Atlantic (including the Gulf of Mexico) and from the Pacific coast of Australia. Initially, we sequenced a spinner shark from Australia and predicted that *Rsa*I would not cut the diagnostic fragment. We restricted fragments from seven spinner sharks, two from Australia, and five from the U.S. Atlantic and Gulf of Mexico coasts. Although fragments from the two spinner sharks from Australia were not cut with *Rsa* I, each of the five specimens from the Atlantic produced fragments of 251 and 144 bp. We sequenced one specimen from the Atlantic (spinner B) and found two nucleotide substitutions, including one that resulted in the restriction site difference between spinner sharks from the Atlantic and Pacific.

We detected numerous differences between restriction patterns predicted from the sequence of Martin and Palumbi (1993) for tiger shark collected near Hawaii and our tiger sharks collected from the Gulf of Mexico (Atlantic) and Hawaii and Australia (Pacific).

Table 2 (continued)

```
Cal-A   TAACACAAATCTTCTTCTGACTTCTTGTGGCCAACTCAATTATTTTAACTTGAATTGGAGGTCAACCAGTAGAACAACCA
Cbr-A   ..........T..................A..T..T.............................C...................
Cbr-B   ..........T..................A..T..T.............................C...................
Cfa-A   ............................C..A.................C.................C...................
Cle-A   ..........TC.............C..A..T..T.........................T.....................
Cli-A   ............................A..T..T.....C.........................C.....................
Cob-A   ...G........................A.....T.............................C...................
Cpl-A   ...........................................................................................
Cpl-B   ...........................................................................................
Cpl-C   ...........................................................................................
Gcu-A   ....C......C.........T.C.....A..T........C..CC................C...................
Gcu-B   .T.........................C..A..T..................C............A...................
Nbr-A   .C...................T.......A..T.................................C...................
Sle-A   ............................C..A................CC.................C...................
Smo-A   ....................T.....C.A..T............C.....C...............................

Cal-A   TTCATTATAGTAGGACAAATCGCCTCAATCTCCTACTTTTCCTTATTCCTTATTATTATACCATTCACTAGCTGATGAGA
Cbr-A   .....................T..T.................................C..C.....T..T..C...........
Cbr-B   .....................T..T.................................C..C.........T..C...........
Cfa-A   ..T.....................................G.................................C.........C..
Cle-A   .......C............T.....................................C.........T...............
Cli-A   ...........................................T.......G.C.....................................
Cob-A   ..............T.....................................C..C.......C.T...............
Cpl-A   .....................T.....................................C...................
Cpl-B   ...........................................................................................
Cpl-C   .....................T.....................................C...................
Gcu-A   .....................T.....................A....T...........T......G.C.........C..
Gcu-B   ..T....C............T..T.....................T.....C..C.........T.TC.........C..
Nbr-A   ..T.....................T.....................................T...........T..
Sle-A   ..T....C.................................C..TC....T.....C.............G.C.........C..
Smo-A   ..T.....................................A...........C.............G...........C..

Cal-A   AAACAAAATCCTCAGCCTAAATTAG | TTTTGGTAACTTAACT-AAAAAGCGTCGAC | CTTGTAAGYCGAAGACTGGAG
Cbr-A   ........................... | ........G..................... | .....................
Cbr-B   ........................... | ........G..................... | .....................
Cfa-A   ...T....................... | ........G..................... | .....................
Cle-A   ........................... | ........G..................... | .....................
Cli-A   ........................... | ........G..................... | .....................
Cob-A   ........................... | ........G..................... | .....................
Cpl-A   ........................... | ........G..................... | .....................
Cpl-B   ........................... | ........G..................... | .....................
Cpl-C   ........................... | ........G..................... | .....................
Gcu-A   .........T...........C... | ........G..................... | .....................
Gcu-B   ....................C... | ........G..................... | .....................
Nbr-A   ...T....................... | ........G..................... | .....................
Sle-A   .........T...........C... | .......GG.........-........... | .....................
Smo-A   .........T...........C... | .......GG.....T.CGT........... | .....................

                                                                    <-  Cb6H  3'
```

We sequenced a tiger shark from the Gulf of Mexico and found 46 nucleotide differences between our sequence and that of Martin and Palumbi (1993). This difference is greater than that seen between all pairs of species in this study and is clearly too large of a difference to be explained by intraspecific polymorphism. Because our observed restriction patterns for tiger sharks from the Atlantic and Pacific match predictions made from our tiger shark sequence, our sequence for the tiger shark is likely correct, and part of the sequence listed in Martin and Palumbi (1993) is not that of tiger shark.

The remaining eight species—bignose, blacktip (*C. limbatus*), bull (*C. leucas*), dusky, silky (*C. falciformis*), scalloped hammerhead, great hammerhead, and lemon sharks—exhibited restriction patterns

identical to those predicted based on sequence data (Table 4). The list of species that showed no variation in restriction pattern included silky and dusky sharks from widely disparate geographic locales.

Discussion

Restriction digests of the diagnostic 394–396 bp fragment proved a reliable way to distinguish among the

Table 3

Predicted restriction fragments for seven enzymes based on nucleotide sequences.

Species	*Alu*I	*Dde*I	*Fok*I	*Hae*III	*Hinc*II	*Hinf*I	*Rsa*I
Bignose	232, 84, 79	331, 64	310, 85	205, 190	223, 148, 24	324, 71	251, 144
Blacktip	121, 111, 79, 43, 41	333, 64	395	395	223, 148, 24	324, 71	251, 144
Bull	190, 121, 43, 41	331, 64	395	395	223, 148, 24	324, 71	251, 144
Dusky	311, 43, 42	331, 64	395	221, 174	371, 24	324, 71	395
Sandbar A	223, 79, 43, 41	331, 64	395	205, 190	223, 148, 24	324, 71	251, 144
Sandbar B	223, 79, 43, 41	331, 64	310, 85	205, 190	223, 148, 24	324, 71	251, 144
Sandbar C	223, 79, 43, 41	331, 64	310, 85	205, 190	223, 148, 24	324, 71	251, 144
Silky	232, 79, 43, 41	331, 64	310, 85	221, 174	371, 24	324, 71	395
Spinner A	190, 121, 43, 41	331, 64	395	221, 174	371, 24	324, 71	395
Spinner B	190, 121, 43, 41	331, 64	395	221, 174	371, 24	324, 71	251, 144
Lemon	190, 121, 43, 41	331, 64	310, 85	221, 174	371, 24	324, 71	395
"Tiger" A[1]	190, 121, 43, 41	331, 64	208, 187	221, 174	371, 24	216, 108, 71	251, 144
Tiger B	190, 121, 43, 28, 13	331, 64	310, 85	395	371, 24	395	395
Great Hammerhead	121, 111, 85, 89	331, 65	396	396	223, 149, 24	325, 71	396
Scalloped Hammerhead	311, 83	256, 75, 63	394	221, 173	370, 24	323, 71	395

[1] It was determined that this sequence was not that of a tiger shark. See text.

Table 4

Number and location of sharks whose mtDNA was subjected to restriction enzyme digestion. Numbers in parentheses represent number of sharks from each source location in the sample.

Species	*n*	Source of specimen
Bignose shark	4	Virginia, Atlantic Ocean (4)
Blacktip shark	7	Virginia, Atlantic Ocean (1); Florida, Gulf of Mexico (6)
Bull shark	7	Florida, Gulf of Mexico (7)
Dusky shark	7	Virginia, Atlantic Ocean (2); Florida, Atlantic Ocean (1); Australia, Pacific Ocean (3); Australia, Indian Ocean (1)
Lemon shark	7	Florida, Gulf of Mexico (6); Mexico, Gulf of Mexico (1)
Sandbar shark	10	Florida, Gulf of Mexico (7); Hawaii, Pacific Ocean (3)
Silky shark	7	Texas, Gulf of Mexico (3); Hawaii, Pacific Ocean (4)
Spinner shark	7	Virginia, Atlantic Ocean (1); Florida, Atlantic Ocean (3); Florida, Gulf of Mexico (1); Australia, Pacific Ocean (2)
Tiger shark	10	Florida, Gulf of Mexico (5); Australia, Pacific Ocean (2) Hawaii, Pacific Ocean (3)
Great hammerhead	7	Florida, Gulf of Mexico, Florida (6); Florida, Atlantic Ocean (1)
Scalloped hammerhead	7	Virginia, Atlantic Ocean (1); Florida, Gulf of Mexico (2); Alabama, Gulf of Mexico (1); Texas, Gulf of Mexico (1); Campeche, Gulf of Mexico (2)

eleven species of carcharhiniform sharks. Each species possessed a unique set of restriction fragments, and even in the species where polymorphism was detected, misidentification was not a problem. This technique can be performed on small pieces of tissue collected at dockside and stored indefinitely at room temperature and moreover can distinguish between species whose carcasses may be difficult to discriminate (Fig. 1). Similar DNA technology has been used for identifying carcasses in teleosts (Chow et al., 1993; Bartlett and Davidson, 1991), and for identifying planktonic fish eggs (Daniel and Graves, 1993)—cases where morphological characters proved insufficient for species level identification .

Use of genetic characters to identify species can be complicated by population structure. Although most marine fishes that are distributed across vast geographic stretches are open-ocean pelagics (Briggs, 1960), with presumed minor genetic differences across the range of a species (but see Crosetti et al., 1994; Graves et al., 1992), many large coastal sharks are distributed as multiple discrete populations (Compagno, 1984). It is thus important to know whether genetic differences among individuals are diagnostic of species or populations. Some questions, among others, are the following: to what degree are published genetic data useful in regions other than those from which the original specimens were collected, and can this method be used to identify populations as well as species? Baker et al. (1996), for example, were able to determine geographic origin of marine mammals they identified from flesh samples on the basis of genetic data. In our study, regional differences in restriction patterns were observed in only one species, spinner shark, whereas sequence differences that did not affect restriction patterns were observed in sandbar shark. In four species (dusky, silky, scalloped hammerhead, and tiger), sequences from one individual accurately predicted restriction sites in specimens collected thousands of kilometers from where the original specimen was collected.

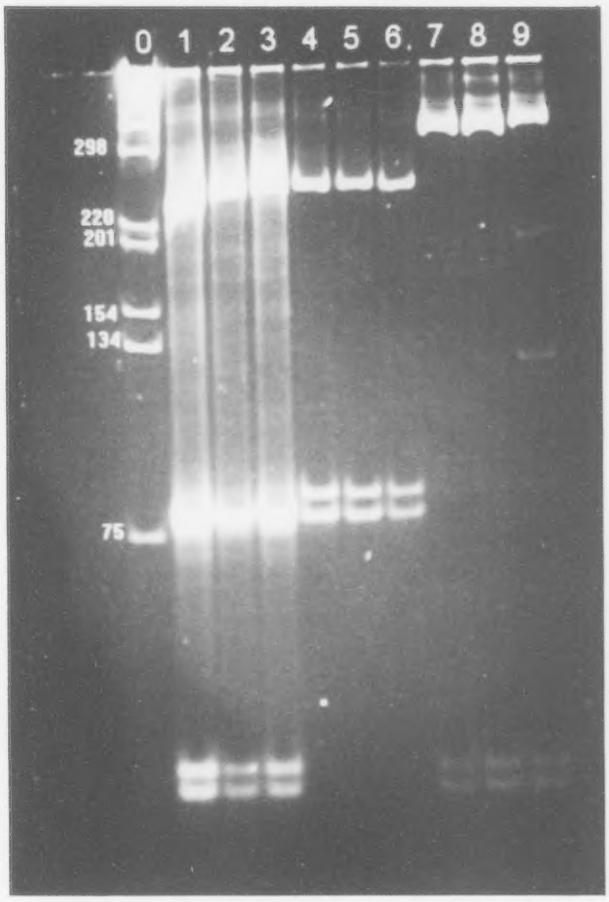

Figure 1

Ten-percent polyacrylamide gel of *Alu*I digests in three species that produce very similar carcasses. Lane zero is a size standard, lanes one to three are sandbar sharks, lanes four to six are bignose sharks, and lanes seven to nine are dusky sharks. Numbers at left refer to sizes (base pairs) of size standards. Predicted sizes of fragments in each species are given in Table 3.

The low level of intra- and interregional polymorphism within species is not surprising given the low genetic diversity typically reported for sharks (Smith, 1986). In restriction fragment length polymorphism (RFLP) studies of whole mtDNA molecules, Heist et al. (1995, 1996) found a very low nucleotide sequence diversity of 0.036% in sandbar shark and 0.13% in Atlantic sharpnose shark (*Rhizoprionodon terraenovae*). The small numbers of substitutions between geographically distant populations of sandbar and spinner shark observed in this study indicate that intraspecific diversity should not hinder species identification of these eleven species.

The erroneous tiger shark sequence in the study of Martin and Palumbi (1993) indicates a further strength of the PCR-RFLP technique beyond use for forensic identification; it can be used to evaluate

validity of sequence data. Many molecular genetic or phylogenetic studies (or both) are based on sequences sampled from only one individual of a species. Discovery of erroneous sequence data in such studies is becoming increasingly common (Derr et al., 1992; Helbig and Seibold 1996; Ledje and Arnason, 1996). PCR reactions are easily contaminated by carryover DNA from other organisms or by other DNAs in the laboratory (Thomas, 1994). Mislabeling of tubes also can lead to incorrect assignment of sequence data to species. We sequenced the entire cyt *b* gene in tiger shark from Florida and, in comparison with the "tiger shark" sequence reported by Martin and Palumbi (1993), found one nucleotide difference in the first (5'-most) 540 bp of the gene and 64 nucleotide differences in the remaining 606 bp of the gene. We hypothesize that the "tiger shark" sequence of Martin and Palumbi (1993) is a mixture that includes sequence data from another species. The discrepancy between published and newly determined sequences is similar to observations on published bird sequence by Helbig and Seibold (1996) and on mammalian sequences reported by Ledje and Arnason (1996). In each case, the published sequences differed so greatly from newly obtained sequences that conclusions of the prior works were called into question. The free exchange of sequence data through Genbank also facilitates replication of errors. Validity of sequence data can, and perhaps should, be tested by amplifying DNA from several individuals of the same species, and then by determining whether predicted restriction sites are present in all amplifications.

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Influence of temperature and effort on lobster catches at different temporal and spatial scales and the implications for stock assessments

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Abstract.—Correlation analysis was used to investigate how effort and temperature changes influence lobster catches at different spatial and temporal scales and how they may affect the use of catch statistics in stock assessments. At the largest scales examined (Atlantic coast of Nova Scotia, 50 yr), a significant correlation between catches and temperatures at short lags (0–3 yr) prior to 1974 suggests that catches were driven by temperature-induced changes in growth or lobster activity. However, changes in effort could not be ruled out as a cause of the observed cycles because sea surface temperatures may reflect weather conditions and the "fishability" of the grounds. Longer lags (6–8 yr) after 1974 are consistent with increased larval survival due to sharply rising temperatures and the "recruitment pulse" of the late 1980s. There was no clear relation between temperature and catches at intermediate scales (statistical districts, 10 yr), but effort changes indicate that catches alone do not accurately reflect changes in lobster abundance. At the smallest scale examined (distances between ports, days) correlations of both temperature and effort with catch in areas with similar coastal topographies indicated that the correlation between temperature and catch was not causative, i.e. changes in effort, were driven by wind events that were also influencing water temperatures. The results indicate that effort changes must be considered at all scales in stock assessments, but they become increasingly important at the smallest (i.e. <100 km, within years) scales. They also indicate that significant correlations between lobster catches and environmental parameters must be interpreted cautiously.

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Fish. Bull. 97: 62–70 (1999).

In the absence of suitable effort data, long-term, large-scale changes in American lobster (*Homarus americanus*) populations are generally assessed by using summarized catch statistics (e.g. Harding et al, 1983; Pezzack, 1992; Drinkwater et al, 1991, 1996), under the assumption that catch trends reflect abundance changes. Two observations support this assumption. First, high exploitation rates in most areas probably remove the majority of animals recruiting to the fishery in any year (Miller et al, 1985). Second, similar catch trends over large areas of the Northwest Atlantic suggest a similar population response to a common environmental influence (Pezzack, 1992). Given that this assumption is correct at these large scales, it is of fundamental interest in survey design and data aggregation decisions to determine the spatial and temporal scales at which this assumption holds. For example, can the catch statistic alone be used to assess changes in lobster populations between, say, adjacent ports within seasons?

To understand the spatial and temporal variability of lobster catches on the Atlantic coast of Nova Scotia, Canada, and the underlying causes of this variability, I examined the influence of effort and an important environmental factor (temperature) on commercial lobster catches at different spatial and temporal scales. Temperature can affect lobster catches in the short term by altering the availability of lobsters to traps, i.e. by changing lobster behavior on the grounds (McCleese and Wilder, 1958) or by increasing growth of prerecruits to commercial sizes. In the long term it could also affect population growth by influencing survival of larvae or juvenile stages (Aiken and Waddy, 1986). Changes in effort affect lobster catches directly but how these changes occur is complex. In a lucrative fishery with a relatively short (approx. 60 d) open season and restrictions on the number of traps, fishermen tend to take the maximum number of lobsters possible with their gear. Consequently, changes in effort are more likely to be due to factors that decrease effort. For example, fishermen could decrease the number of traps fished and frequency of hauls when catches are too low to make fishing worthwhile. Because the fishery is conducted from small boats, adverse weather conditions will also decrease effort. Conversely, fishermen may respond to increasing catch rates or good weather by fishing harder. Because catches alone are often used as an indication of stock status, it is important to understand how changes in effort may be influencing catches at the different spatial and temporal scales at which assessments are conducted.

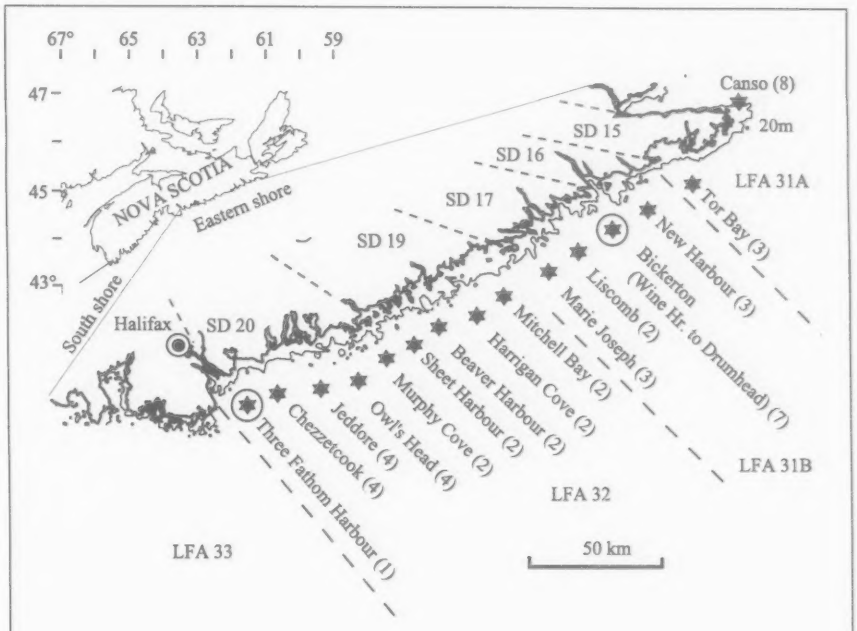

Figure 1

Study area, including locations of ports along the eastern shore where fishermen provided catch and effort information. The number of index fishermen at each location providing data in 1994 is given in brackets after the port name. The dashed lines show the boundaries between lobster fishing areas (LFAs) and statistical districts (SDs). The location of ports that are discussed in the text are circled.

Materials and methods

Annual lobster catch is recorded by statistical district from purchase slips by the Department of Fisheries and Oceans (DFO). These data are summarized by larger geographical units for assessment purposes, usually by lobster fishing areas (LFAs). In order to examine the large scale relationships between catches and temperature, catches were summarized in a similar manner for this analysis. The Atlantic coast of Nova Scotia (Fig. 1) was bisected into coastlines of approximately equal length, named the eastern shore (LFAs 31A, 31B, and 32) and south shore (LFA 33). Long-term records of sea surface temperatures (SSTs) are available from Halifax harbour which is located on the boundary between these areas and can be considered representative of both.

The three data series, i.e. total annual catches from the south and eastern shore and average annual SSTs, were smoothed with a 3-yr running average. Examination of the plots suggested that the series could be divided into two periods, a pre-1974 period of high-frequency, low-amplitude cycles, and a single post-1974 cycle of high amplitude. Correlations at lags of 0–10 years were then run for each period separately and combined.

Daily catch and effort information is collected for DFO by selected index fishermen in some areas of Nova Scotia. At minimum these fishermen provide total lobster catches (usually weight in pounds) and the number of traps hauled on a daily basis during the fishing season. The number of index fishermen varies between areas but tends to cluster around key ports that are also sampled for length frequencies by port samplers. On the eastern shore, about 20 fishermen have kept log books along a 200-km stretch of coastline between Canso and Halifax, some beginning as early as 1986. In 1994 an additional 28 fishermen associated with the Fishermen's and Scientists' Research Society (FSRS) kept logs in this area. Most FSRS fishermen also deployed continuous temperature recorders (Vemco Ltd., Halifax, N.S.) on their traps during the 1994 fishing season, which extended from 20 April to 20 June in LFAs 31B and 32, and from 1 May to 31 June in LFA 31A. Because effort information is available only for a limited num-

Table 1
Statistics for correlation analysis of data series in Figure 1.

	Eastern shore			South shore		
	significant lags (yr)	lag (yr) at maximum r	r	significant lags (yr)	lag (yr) at maximun r	r
Pre-1974	1–3	2	0.683*	0–2	1	0.688*
Post-1974	—	8	0.519	—	6	0.532

* = significant at $P<0.01$.

ber of index fishermen within each statistical district, total effort for each district was calculated by dividing its total catch by the average catch per trap haul (CPTH) for index fishermen in that district.

Because seasonal trends were evident in temperature, CPTH, and effort data, any analysis involving daily observations of these parameters were detrended by using first differencing i.e. $i - (i - 1)$, where i is the individual observation of temperature, CPTH, or catch. This avoided spurious negative correlations between the decreasing catches throughout the season that were due to depletion of the fishable biomas, and increasing spring–summer temperatures. Because most fishermen on the eastern shore attempt to haul their traps daily and because longer soaks are usually associated with unfavorable weather (which tends to affect most fishermen in the same area), there was no attempt to adjust for differences in soak times within or between each fisherman's time series. Inspection of the data showed that gaps in the individual time series tended to occur on the same days, which coincided with storm days and Sundays.

Temperature information was also available from DFO moored recorders moored along the eastern shore during the period when logbooks were kept. Years with a strong association between temperature and catch were identified for further study at smaller spatial and temporal scales as follows: daily, temperature, catch, and effort data from the 1986–94 fishing seasons at the location with the most complete longer-term records, i.e. Port Bickerton, were detrended as described above and the resulting individual series correlated. This analysis identified 1991 and 1994 as years with significant correlations. The latter year was chosen for further investigation into the nature of this relationship because of the availability of data at small spatial scales throughout the area from FSRS records. Three matrices of port versus date, one each for the detrended temperature, CPTH and effort data, were then developed for further correlation analysis. Each matrix resulted in a port versus port matrix of correlation coefficients, i.e indices of similarity between port pairs in terms of the daily patterns of change for the respective parameters. Correlations between port pairs could then be plotted against distance between them.

Results and discussion

Effort information is not available at the largest spatial and longest temporal scale examined (Atlantic coast of Nova Scotia, 50 years). At this scale, however, there is a significant correlation between annual mean sea surface temperatures in the approximate center of the area (i.e. Halifax harbor) and summarized lobster catches (Fig. 2; Table 1) at short lags prior to 1974. This correlation was also noted by Campbell et al (1991). Catches are significantly correlated ($P<0.01$) with temperatures for three cycles prior to 1974 at lags of 1–3 years on the eastern shore and 0–2 years on the south shore. After 1974, correlations are highest (although marginally insignificant) at lags of 8 years on the eastern shore and 6 years on the south shore, approximately the time lobsters take to recruit to the fishery in these areas. This finding suggests that during this period, temperature or an unknown covariate also influenced the survival of larvae and subsequently increased recruitment to the fishery. The increase in catches in both areas after 1974 is consistent with the northwest Atlantic coast-wide "recruitment pulse" (Pezzack 1992), which is generally attributed to a common environmental influence, although Drinkwater et al (1996) concluded that this environmental influence was not temperature. Prior to 1974 the near in-phase changes in temperature and catch along the eastern and south shore could be due to temperature-induced changes in catchability during warmer years i.e. to greater activity of lobsters on the grounds or faster growth to legal size, or to both. However, without long-term effort information, changes in effort cannot be

ruled out as a cause of the pre-1974 catch cycles. For example, because Halifax harbour sea surface temperatures reflect weather conditions in the study area, years with colder sea surface temperatures could also be years with less fishing activity. It is noteworthy that along the eastern shore both pre- and post-1974 catches lag temperatures by 1–2 yr longer than on the south shore. Hudon (1994) noted that the population along the eastern shore may be growth-limited owing to colder water temperatures than those in adjacent areas, and one would expect this area to react more slowly to the more moderate temperature increases.

Catch and effort in smaller statistical districts along the eastern shore, along with available temperature indices in the area (Fig. 3), reflect the catch patterns of most other lobster fishermen in the northwest Atlantic during this period, i.e. peak catches in the late 1980s and subsequent declines. There was an increase in effort along the eastern shore throughout the period. There is no apparent relation between catches and available temperature indices, although the warmest water and highest catch both occurred in the same year (1989).

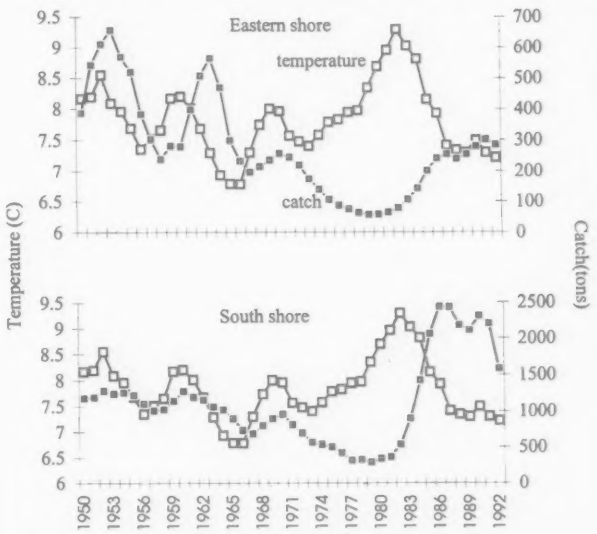

Figure 2

Total annual lobster catch for the eastern shore and south shore of Nova Scotia and average annual sea surface temperatures in Halifax harbor, 1950–92. All data series were smoothed with a three year average.

Port Bickerton reflected the catch and effort pattern of the eastern shore as a whole, including an increase in effort throughout most of the period (Fig. 4). Note that the increase in the average daily number of trap hauls leveled off when catches started to decline after 1991. Perhaps fishermen were increasing effort in response to increasing lobster catches during the 80s. Pringle and Duggan (1984) noted that as many as 25% of the maximum number of traps (eastern shore trap limit is 250) can remain unused in the Nova Scotia lobster fishery. Although the use of catches alone would have overestimated the rate of increase in the population during the 80s and underestimated the subsequent decline, the differences are small and would not have affected conclusions on annual population changes.

A significant correlation between average daily temperatures and CPTH at Port Bickerton occurred in only 2 of the 8 years for which temperature, catch, and effort information is available at this scale, suggesting that short-term, temperature-induced changes in catchability occurred, or were detectable, during those years (Tables 2 and 3). However, a multiple regression of daily catch (dependent variable) versus effort and temperature during these years also indicates that short-term changes in lobster catches were largely determined by effort changes. Cross correlations between total daily catch and effort at Port Bickerton at lags of 0–7 days showed no significant correlations at lags other than 0, indicating that fishermen's effort was not influenced by catches at short time scales.

Table 2

Pearson correlation coefficients for average daily temperature (at 10 m) vs. total daily catch, total daily effort, and average daily catch per trap haul for index fishermen at Port Bickerton 1986–94.

	Catch	Effort (trap hauls)	Average CPTH
1986	0.0491	0.1066	0.0830
1987	0.2158	0.0065	0.1740
1988	–0.0380	–0.0373	0.1060
1989	–0.0551	0.0718	0.1580
1990	0.1317	0.1239	0.1690
1991	0.311*	0.1014	0.408*
1992	–0.1426	–0.2853	0.2110
1993[1]			
1994	0.2477	0.1888	0.262*

* = significant at $P<0.05$.
[1] Temperature data for 1993 were not available in Bickerton during the fishing season.

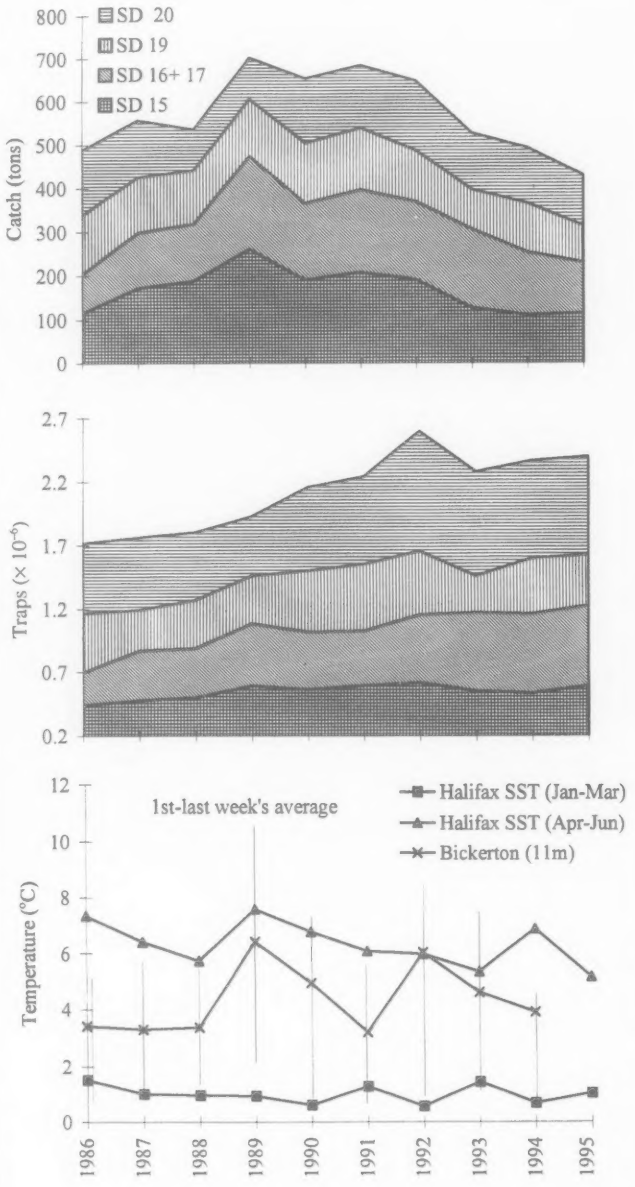

Figure 3

Total annual lobster catch (top) and total annual effort (middle) for eastern shore statistical districts from 1986–95, the years for which effort information is available from index fishermen. Also shown for these years are three temperature indices (bottom), including average sea surface temperatures (SST) in Halifax harbour from January to March; average SST from April to June i.e. during the lobster season; and average water temperatures (11 m) at Port Bickerton during the lobster season. The bars show the average temperature for the first (lower) and last (upper) week of the lobster season.

Correlation coefficients of the daily first differenced CPTH data from individual fishermen on the eastern shore were plotted against distance from Port Bickerton and Three Fathom Harbour (Fig. 5), situated about 125 km apart near the northeastern and southwestern end of the study area (Fig. 1). Correlations were strongest in the immediate vicinity of these ports, decreased to insignificance at about 50 km, then increased to a second maximum at 125 km. This pattern was still apparent when all ports were included in the analysis (Fig. 5, bottom), but the least-squares fit to the polynomial was not as good, perhaps because local factors influence the main spatial trend in other areas. In contrast, short-term changes in water temperature are strongly correlated throughout the area (Fig. 6) because they are caused by wind events that impact the eastern shore as a whole. Apparently, the correlation of catches and temperatures at Port Bickerton in 1994 (Table 2) occurred only at either end of the eastern shore. To determine if this correlation was truly a direct environmental influence on catch, I plotted the daily correlation coefficients of all ports against distance separately for CPTH and effort (Fig. 7). The fourth-order polynomials fitted to the data are similar for both, indicating that the similarity in catches between ports on either end of the eastern shore and their similarity to short-term temperature changes are mainly due to similarities in the daily pattern of change in effort. This is confirmed by plotting the coefficients for effort versus temperature directly. Similar results were obtained for 1991, the other year in which significant correlations between temperature and catches were found at Port Bickerton. The reason why fishermen separated by 125 km have similar day-to-day fishing patterns is apparent when one examines the nature of the coastline along the eastern shore (Fig. 1). The coast near Three-Fathom Harbour and Bickerton is characterized by relatively long and narrow bays generally oriented in a north–south direction, which offer more shelter than the relatively exposed coastline between them. If the winds that cause temperature decreases are also those that make fishing more difficult,

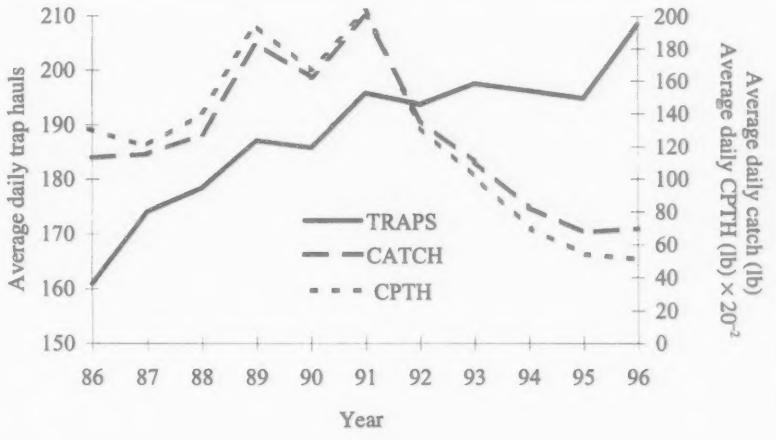

Figure 4

Annual averages of daily catch, trap hauls, and catch per trap haul for index fishermen at Port Bickerton 1986–96.

Table 3

Multiple regression analysis of total daily catch (dependant variable), total daily effort (trap hauls) and average daily temperatures for the two years where significant correlations between temperature and catch per trap haul were found (Table 1). Statistics shown include slope and intercept values (B), standard error of B, and regression coefficients (Beta), with their significance levels (Sig. T).

		B	SE B	Beta	T	Sig. T
1991	Effort	1.1382	0.1055	0.8241	10.7840	0.0000
	Temperature	50.9725	62.0185	0.0628	0.8220	0.4148
	(Constant)	–0.9795	34.8649	–0.0280	0.9777	
1994	Effort	0.4000	0.0528	0.7179	7.5760	0.0000
	Temperature	61.3956	51.8943	0.1121	1.1830	0.2423
	(Constant)	–10.4788	28.9416	–0.3620	0.7188	

e.g. those that are southerly and enter directly into the bays, and are of a minimum force, or both, one would expect a positive correlation between water temperatures and catches in these areas. The apparently spurious correlation between lobster catches and temperature would be weaker in the exposed central area where fishing activity is vulnerable to winds from a wider direction and of less force than those which significantly impact near-shore water temperatures. Although it is clear that the observed correlations between short-term changes in lobster catches and temperatures are strongly influenced by changes in effort, these results do not rule out a concurrent direct affect of temperature on lobster activity and catches, i.e. effect of catchability. Possibly fishermen are aware that winds of a certain direction and force affect lobster activity and catchability and alter their fishing activity accordingly, or the factors that decrease fishing activity also decrease lobster catchability independently.

These results indicate that although changes in effort can influence lobster catches at all spatial and temporal scales examined, data on effort is particularly critical in correctly interpretating the meaning of changes in catch at smaller scales i.e. <100 km and <1 yr. In particular, they indicate that small-scale correlations between environmental parameters such as winds and water temperatures with lobster catches alone should be treated cautiously because inferences made about their underlying mechanisms may be wrong. For example, Hudon (1994) concluded that differences in annual catches between approximately 100-km lengths of the Nova Scotia coastline were due to differences in the orientation of these coastlines to upwelling winds, the resultant change in wa-

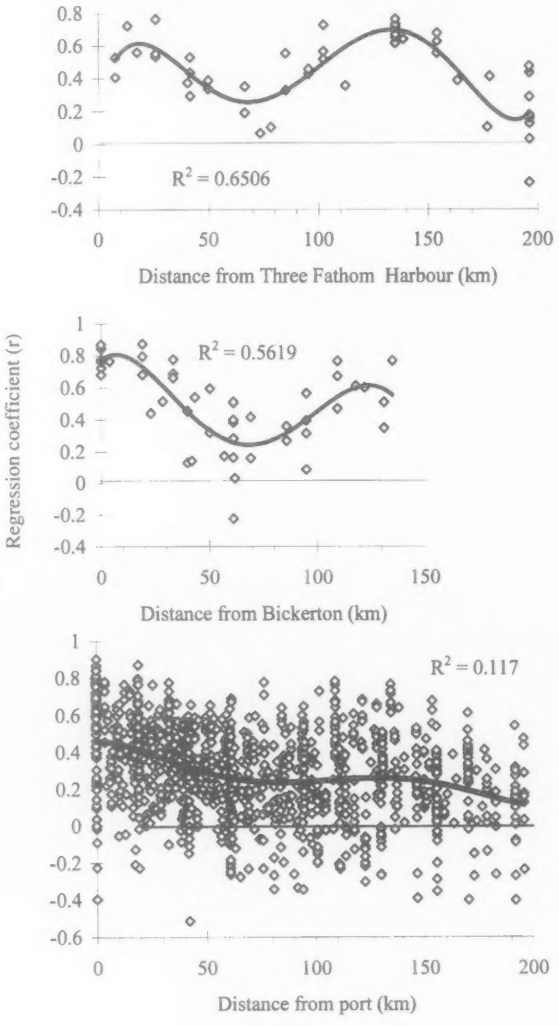

Figure 5

Pearson correlation coefficients of first differenced daily CPTH of all index fishermen along the eastern shore versus increasing distance from Three Fathom Harbour (top) and Bickerton (middle). The bottom figure plots the same statistic for all ports versus distance from each other. A fourth order polynomial provided the best least-squares fit to each data set.

ter temperature, and the effect of the latter on lobster productivity. This study suggests that at least some of these differences may be due to differences in effort and "fishability" of the coastlines involved.

These results also give a general indication of the sampling effort (i.e. number of index fishermen) and distribution (spacing of index fishermen) required of a program whose objective is to characterize and assess changes in effort for an entire coastline. Because changes in effort from index fishermen separated by short distances, i.e. within the working reaches of a fishing port, are strongly correlated, it would be more effective for any given total sampling intensity to space samples evenly along that coastline, rather than cluster them in ports. Since the correlation of index fishermen's catch data decreases quickly at dis-

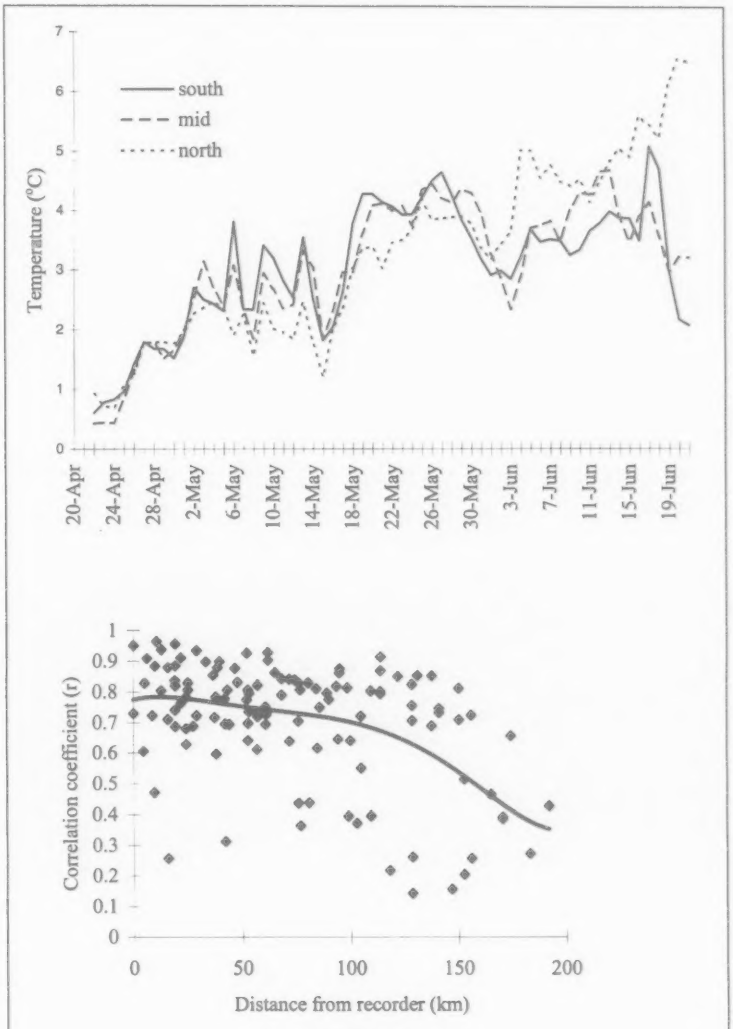

Figure 6

(Top) Average daily temperatures from temperature recorders deployed by index fishermen on their traps during 1994, for the southern (south of Murphy Cove), middle (Murphy Cove to Liscomb) and northern (north of Liscomb) sections of the eastern shore. (Bottom) Pearson correlation coefficients of first differenced temperature data from all temperature recorders deployed by index fishermen versus distance between instruments in 1994.

tances greater than about 25 km, the samples should be more closely spaced. On the eastern shore, where the annual average number of fishermen providing information is about 20, the resulting 10-km spacing at this sampling level should be adequate to provide a representative sample.

Although these results have not eliminated the possibility of temperature-induced changes in catchability, they do indicate that quantifying these changes with fishermen's data would be extremely difficult.

Acknowledgments

I wish to thank the Nova Scotia lobster fishermen who provided information used in this study, especially those who have collected data since the begin-

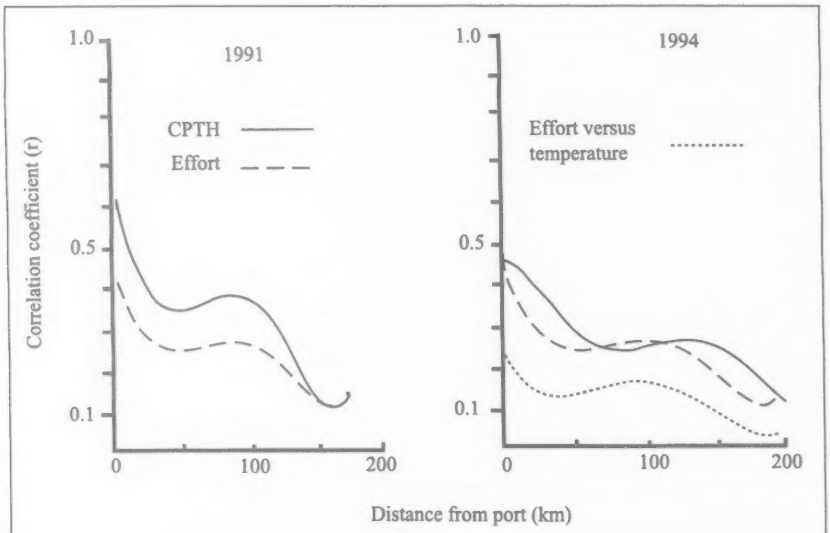

Figure 7

Fourth order polynomials as shown in the bottom of Figure 5, but for catch per trap haul and trap hauls separately, for the years in which significant correlations of daily temperature and catch per trap haul were found at Port Bickerton (1991, 1994). Also shown is the polynomial curve for individual fishermen's daily effort versus daily average temperatures in their area in 1994. Individual points have been omitted for clarity, but their distribution is similar to the bottom of Figure 5.

ning of DFO's lobster logbook program. Their continuing efforts increase the value of this database each year. The cooperation of Randy Baker, Sean Smith, and fishermen of the Fishermen's and Scientists' Research Society is gratefully acknowledged for access to additional data for the 1994 season, including temperatures. Ed Verge provided historical temperature data collected by the Physical and Chemical Sciences Branch, DFO, and Ron Duggan summarized much of the data for analysis. Bob Roger and Steve Smith provided statistical advice, and John Tremblay and Doug Pezzack reviewed early versions. I am particularly indebted to three anonymous reviewers whose suggestions significantly improved the manuscript.

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Abstract.—We evaluated the use of total body electrical conductivity (TOBEC) for determination of whole-body water content of yellow perch, *Perca flavescens*, and alewife, *Alosa pseudoharengus*. We used multiple linear regression with backwards stepwise elimination to test the capability of TOBEC values, wet weight, and total length in predicting whole-body water content of yellow perch and alewife. We found that wet weight was the best predictor of whole-body water content. The inclusion of TOBEC values in multiple linear regressions did not improve the predictive capability of wet weight over simple linear regressions that used wet weight alone (r^2 increased by only 0.00002 to 0.0005). We reanalyzed the data from three previous studies that used TOBEC to evaluate the tissue composition of fish. Again we found that the inclusion of TOBEC values in regression functions with wet weight as the other independent variable did not substantially improve the predictive capability of functions that used wet weight alone (r^2 increased by only 0.00003 to 0.0007).

Evaluation of total-body electrical conductivity to estimate whole-body water content of yellow perch, *Perca flavescens*, and alewife, *Alosa pseudoharengus**

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Attempts to construct energy budgets for many important fish species are often hampered by the lack of data on their energy density. Further, the study of energy flow in aquatic communities is complicated by seasonal variation of the energy density within organisms and relative differences in energy content of predator and prey (Craig, 1977; Stewart et al., 1983; Stewart and Binkowski, 1986; Rand et al., 1994). The shortage of useful data is due in part to the difficulty of determining the energy content of large numbers of individuals. Estimation of fish energy density has been simplified with development of relationships, based on calorimetric analysis, between percentage dry weight ($100 \times$ (dry weight/wet weight)) and wet weight energy density (Stewart and Binkowski, 1986; Rand et al., 1994; Hartman and Brandt, 1995; Lantry, 1997). The measurement of dry weights on substantial numbers of large individual fish, however, can be problematic, because they require considerable time to dry, use large amounts of oven space, and may require time-consuming sectioning or grinding procedures.

Measurement of total body electrical conductivity (TOBEC) has been presented in the literature as a reliable alternative to the sacrifice of organisms to evaluate tissue composition. Lipid content and lean body mass have been accurately estimated by measuring TOBEC in humans, swine, rats and birds (Domermuth et al., 1976; Bracco et al., 1983; Presta et al. 1983; Keim et al., 1988; Walsberg, 1988; Castro et al., 1990). TOBEC has recently been used for the estimation of body composition of three fish species: sunshine bass (a white bass [*Morone chrysops*] $\times$ striped bass [*Morone saxatilis*] hybrid, Brown et al., 1993); red drum (*Sciaenops ocellatus*, Bai et al., 1994); and channel catfish (*Ictalurus punctatus*, Jaramillo et al., 1994).

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In our analyses of fish community dynamics in Lake Ontario and Oneida Lake, New York, we used bioenergetics to evaluate trophic transfer and tissue growth (Rand et al., 1995; Lantry, 1997). To model trophic energy flux accurately, we needed to estimate fish energy content throughout the years being simulated. Because of the difficulty encountered in drying large numbers of fish and in drying large individuals, we sought an alternative method—measurement of whole-body water content. Our objective here was to evaluate the use of TOBEC as an alternative to drying, for estimating the whole-body water content of yellow perch (*Perca flavescens*), an important prey and sport fish component of both lakes, and alewife (*Alosa pseudoharengus*), the dominant planktivore and prey fish in Lake Ontario.

Materials and methods

We used the "EM-SCAN Inc. SA2 Small Research Animal Body Composition Analyzer" to obtain TOBEC values for yellow perch and alewife. The measurement principle of the EM-SCAN has been published elsewhere (Fiorotto et al., 1987; Walsberg, 1988; Brown et al., 1993). The scanner uses a radiating coil to set up a low-frequency electromagnetic field to measure the electrical conductivity of an animal. Because electricity is conducted by the ions dissolved in body water, the most direct relationship that can be drawn from the TOBEC values is the amount of water contained within an animal. By initially measuring the wet weight of a fish and then measuring the whole-body water content with the scanner, we could obtain the dry weight of the fish by difference, and calculate the percentage dry weight, which is the key parameter we needed to estimate energy density.

Sample collection and processing

We collected 43 yellow perch in bottom trawls from Oneida Lake, NY, over four dates in 1992: 23 April, n=10; 9 June, n=5; 30 September, n=10; and 23 November, n=18. We collected 47 alewife from the New York waters of Lake Ontario with a 3-m bag seine on 2 May (n=13) and 4–5 July (n=34) 1993. Yellow perch were kept alive in lake water during sampling, and alewife were placed on ice immediately after capture. All fish were frozen in water upon arrival at the laboratory.

During processing, fish were thawed under warm running water, blotted dry, weighed to the nearest 0.1 g and measured for total length (mm). We obtained TOBEC values according to the procedures outlined in the scanner manual (EM-SCAN Inc., 1991). Because the positioning of the animal is important in obtaining consistent conductivity readings, fish were placed on their right sides headfirst on the animal carrier trays with the portion of their bodies anterior to the distal end of the shortest ray of the pelvic fin lined up in front of the scribed mark on the tray. Each fish was scanned five times in the scanner's fixed mode and the readings were averaged to produce a mean TOBEC value. After scanning, all fish were dried to a constant weight at 65°C.

Statistical analysis

We constructed simple and multiple linear regression models to predict whole-body water content (*WC*, g). Following earlier fish studies (Brown et al., 1993; Bai et al., 1994; Jaramillo et al., 1994) we included wet weight (*WWT*, g), total length (*TL*, mm), and *TOBEC* as independent variables in regressions. We graphed these variables against fish *WC* (determined from drying individuals) to evaluate the shape of the relationships. We transformed independent variables when relationships with *WC* departed from linear trends. We used SYSTAT 5.03 for Windows (1993) to perform stepwise multiple linear regressions with backwards elimination on all variables (inclusion probability: $P \geq 0.15$) to determine which independent variables accounted for most of the variation in predictive equations (Zar, 1984; Neter et al., 1985). The resulting regression models were then used to predict *WC* and calculate percentage error (*PE*):

$$PE = \left\{\left(\left|\text{actual} - \text{predicted}\right| / \text{actual}\right) \times 100\right\}.$$

Finally, we calculated percentage dry weight from both actual (determined from drying) and predicted (from regression equations) water content and compared the variation between these values to the range of percentage dry weights commonly observed for yellow perch and alewife (Tables 1 and 2).

Results

Significant ($P<0.05$) positive relationships were found in simple linear regressions between the dependent variable *WC* and the independent variables *TOBEC*, *WWT*, and *TL* for both yellow perch and alewife (r^2=0.66 to 0.99). Simple linear regressions of *TOBEC* on *WC* produced r^2 values of 0.933 and 0.667 for yellow perch and alewife, respectively. Multiple linear regressions with two independent variables (*WWT* and *TOBEC*) gave excellent fits to the data for both species. The equation for yellow perch was

$$WC = 3.46239 + 0.69844 \times WWT + 0.00559 \times TOBEC \quad (r^2=0.998).$$

Table 1

Yellow perch individual water content (g) from measurements (act) and predicted (pred) from regression functions. TOBEC is the average scanner conductivity index (based on five consecutive measurements). %DWT is the percentage dry weight and is equivalent to: {(| wet weight – water |)/wet weight} × 100. Values in parentheses are percentage errors (PEs) referring to water (g) and %DWT, and are equivalent to {(| actual – predicted |)/actual} × 100.

Total length (mm)	Wet weight (g)	TOBEC	Water (g) (act)	Water[1] (g) (pred)		Water[2] (g) (pred)		%DWT (act)	%DWT[1] (pred)		%DWT[2] (pred)	
196	99.5	138.6	76.8	73.73	(3.99)	76.02	(1.01)	22.81	25.90	(13.51)	23.59	(3.42)
166	66.5	65.6	50.8	50.28	(1.03)	51.30	(0.98)	23.61	24.40	(3.34)	22.86	(3.15)
148	51.0	42.6	39.2	39.32	(0.31)	39.83	(1.61)	23.14	22.90	(1.03)	21.90	(5.36)
157	51.2	40.4	39.2	39.45	(0.63)	39.79	(1.50)	23.44	22.95	(2.07)	22.29	(4.91)
160	57.1	48.8	44.0	43.62	(0.87)	44.18	(0.42)	22.94	23.61	(2.93)	22.62	(1.40)
151	46.8	28.2	35.6	36.31	(1.99)	35.94	(0.95)	23.93	22.42	(6.31)	23.21	(3.02)
137	31.4	17.6	25.2	25.49	(1.16)	25.00	(0.81)	19.75	18.82	(4.71)	20.40	(3.31)
141	35.0	20.8	27.2	28.02	(3.03)	27.66	(1.68)	22.29	19.93	(10.57)	20.98	(5.86)
133	27.9	12.8	21.7	23.02	(6.08)	22.14	(2.05)	22.22	17.49	(21.30)	20.63	(7.12)
135	29.7	14.6	23.3	24.29	(4.24)	23.54	(1.02)	21.55	18.22	(15.43)	20.75	(3.70)
239	223.1	346.6	154.7	161.22	(4.20)	161.76	(4.54)	30.64	27.73	(9.49)	27.49	(10.28)
275	288.6	481.9	199.8	207.73	(3.96)	206.90	(3.55)	30.76	28.02	(8.92)	28.31	(7.99)
265	296.6	466.8	204.2	213.23	(4.43)	211.67	(3.66)	31.16	28.11	(9.79)	28.64	(8.09)
271	290.3	415.9	203.4	208.55	(2.54)	206.44	(1.51)	29.94	28.16	(5.95)	28.89	(3.52)
229	210.9	361.5	151.4	152.79	(0.88)	154.37	(1.93)	28.19	27.56	(2.25)	26.81	(4.91)
242	284.6	642.5	204.6	205.83	(0.57)	207.73	(1.51)	28.10	27.68	(1.50)	27.01	(3.88)
258	301.5	586.0	217.5	217.32	(0.09)	217.39	(0.06)	27.86	27.92	(0.23)	27.90	(0.15)
256	260.2	538.4	198.2	188.21	(5.03)	190.02	(4.12)	23.84	27.67	(16.08)	26.97	(13.16)
261	280.0	561.7	210.9	202.17	(4.12)	203.15	(3.65)	24.69	27.80	(12.57)	27.44	(11.15)
201	106.2	108.3	82.1	78.24	(4.64)	78.94	(3.79)	22.74	26.33	(15.78)	25.67	(12.89)
195	101.1	96.8	77.3	74.62	(3.50)	75.12	(2.85)	23.51	26.20	(11.40)	25.70	(9.28)
209	132.9	155.2	100.4	97.15	(3.20)	98.03	(2.32)	24.48	26.90	(9.88)	26.24	(7.17)
205	139.6	179.1	107.4	101.97	(5.04)	103.23	(3.86)	23.08	26.96	(16.80)	26.05	(12.87)
163	54.6	36.2	39.1	41.80	(6.82)	41.62	(6.37)	28.33	23.44	(17.26)	23.77	(16.11)
144	41.8	24.2	31.8	32.79	(3.11)	32.36	(1.74)	23.91	21.55	(9.88)	24.34	(5.88)
156	45.4	26.8	34.5	35.32	(2.37)	34.91	(1.18)	24.00	22.20	(7.51)	23.10	(3.75)
147	40.6	22.1	31.2	31.94	(2.44)	31.37	(0.61)	23.20	21.32	(8.08)	22.73	(2.03)
131	27.9	11.0	21.6	23.01	(6.34)	21.88	(1.14)	22.44	17.53	(21.90)	21.56	(3.92)
128	26.4	10.8	20.6	21.96	(6.42)	20.90	(1.26)	21.83	16.81	(22.99)	20.84	(4.52)
116	17.6	5.8	13.8	15.79	(14.35)	14.40	(4.32)	21.55	10.30	(52.22)	18.16	(15.74)
127	23.7	10.0	18.8	20.07	(6.64)	19.05	(1.21)	20.59	15.31	(25.62)	19.62	(4.68)
129	25.7	11.2	20.4	21.48	(5.30)	20.51	(0.57)	20.64	16.44	(20.37)	20.19	(2.18)
224	172.2	222.2	130.7	124.99	(4.37)	125.58	(3.93)	24.10	27.42	(13.77)	27.08	(12.36)
215	138.4	156.3	105.8	100.97	(4.60)	101.56	(4.04)	23.50	27.02	(14.97)	26.60	(13.15)
281	285.9	378.8	211.9	205.24	(3.13)	202.67	(4.34)	25.88	28.20	(8.96)	29.10	(12.42)
294	387.6	818.4	281.3	278.74	(0.92)	276.73	(1.63)	27.42	28.08	(2.43)	28.60	(4.32)
173	83.0	79.2	62.0	61.90	(0.11)	62.65	(1.10)	25.37	25.45	(0.34)	24.55	(3.22)
227	183.4	273.3	130.6	133.11	(1.94)	134.36	(2.89)	28.81	27.43	(4.79)	26.76	(7.15)
240	237.5	407.6	167.4	171.60	(2.49)	172.50	(3.03)	29.49	27.74	(5.95)	27.36	(7.25)
272	295.5	592.5	215.6	213.10	(1.16)	213.67	(0.91)	27.02	27.86	(3.12)	27.68	(2.47)
278	333.7	784.7	233.4	240.89	(3.23)	241.71	(3.58)	30.06	27.80	(7.52)	27.56	(8.33)
339	434.2	1165	314.3	313.26	(0.32)	312.02	(0.71)	27.63	27.86	(0.83)	28.14	(1.86)
Mean PE's					(3.33)		(2.23)			(10.60)		(6.59)

[1] Predicted (pred) values from the regression function with wet weight (g) and TOBEC as the independent variables.
[2] Predicted (pred) values from the regression function with wet weight (g) and square root transformed scanner conductivity index as the independent variables.

Table 2

Alewife individual water content (g) from measurements (act) and predicted (pred) from regression functions. TOBEC is the average scanner conductivity index (based on five consecutive measurements). %DWT is the percentage dry weight and is equivalent to {(| wet weight – water |)/wet weight} × 100. Values in parentheses are percentage errors (PEs) referring to water (g) and %DWT and are equivalent to {(| actual – predicted |)/actual} × 100. Predicted (pred) values are from the regression function with wet weight (g) and TOBEC as the independent variables.

Total length (mm)	Wet weight (g)	TOBEC	Water (g) (act)	Water (g) (pred)		%DWT (act)	%DWT (pred)	
153	22.85	11.0	18.24	18.70	(2.49)	20.15	18.16	(9.88)
158	27.68	17.0	22.25	22.53	(1.25)	19.62	18.61	(5.14)
166	28.11	14.2	23.69	23.02	(2.83)	15.73	18.12	(15.17)
160	27.02	12.2	21.65	22.18	(2.45)	19.87	17.91	(9.87)
163	29.08	17.4	23.77	23.69	(0.33)	18.24	18.51	(1.50)
164	27.92	13.4	22.29	22.89	(2.72)	20.18	18.01	(10.74)
163	30.41	17.4	23.18	24.82	(7.10)	23.78	18.37	(22.75)
149	22.83	10.6	19.09	18.70	(2.04)	16.38	18.08	(10.42)
163	28.92	15.8	23.99	23.63	(1.48)	17.06	18.28	(7.18)
156	24.91	15.0	20.47	20.27	(0.96)	17.83	18.62	(4.45)
142	20.87	13.8	16.51	16.90	(2.36)	20.89	19.02	(8.95)
155	22.86	12.2	18.93	18.66	(1.42)	17.21	18.39	(6.81)
156	21.14	10.2	17.58	17.29	(1.64)	16.86	18.22	(8.07)
186	41.05	19.6	33.78	33.74	(0.11)	17.71	17.81	(0.53)
183	47.84	26.6	37.94	39.19	(3.29)	20.70	18.09	(12.60)
168	37.97	17.0	30.58	31.25	(2.20)	19.48	17.71	(9.08)
178	40.16	23.2	33.42	32.83	(1.76)	16.79	18.25	(8.70)
171	31.80	13.8	26.25	26.16	(0.33)	17.46	17.74	(1.56)
168	31.88	13.6	26.81	26.23	(2.17)	15.88	17.70	(11.48)
166	32.07	15.4	25.90	26.32	(1.63)	19.25	17.93	(6.85)
166	32.49	12.2	26.94	26.81	(0.47)	17.08	17.47	(2.29)
158	32.83	13.8	27.62	27.04	(2.12)	15.87	17.66	(11.25)
174	40.39	20.4	33.58	33.15	(1.29)	16.86	17.93	(6.36)
148	27.02	11.4	21.71	22.21	(2.34)	19.66	17.78	(9.55)
160	34.66	14.6	27.41	28.55	(4.16)	20.92	17.64	(15.71)
176	32.51	11.8	27.31	26.85	(1.69)	15.99	17.41	(8.89)
175	37.82	16.8	31.31	31.13	(0.58)	17.21	17.70	(2.80)
159	27.34	13.6	22.81	22.39	(1.85)	16.56	18.10	(9.35)
166	40.33	16.6	33.16	33.26	(0.30)	17.77	17.52	(1.39)
171	37.15	16.0	30.78	30.60	(0.59)	17.16	17.64	(2.83)
172	37.97	21.6	31.04	31.04	(0.00)	18.24	18.24	(0.02)
162	32.89	16.0	26.38	26.99	(2.31)	19.80	17.95	(9.34)
180	44.45	21.0	36.61	36.56	(0.12)	17.65	17.75	(0.55)
170	37.20	16.2	29.65	30.63	(3.30)	20.29	17.66	(12.95)
177	39.38	18.2	32.54	32.38	(0.48)	17.36	17.76	(2.28)
141	21.28	10.2	17.48	17.41	(0.39)	17.88	18.20	(1.80)
165	33.97	20.4	28.37	27.71	(2.32)	16.49	18.43	(11.77)
172	42.46	23.4	35.99	34.77	(3.38)	15.25	18.11	(18.79)
157	31.02	16.6	24.79	25.38	(2.38)	20.10	18.19	(9.47)
161	38.78	19.2	32.26	31.84	(1.33)	16.80	17.91	(6.58)
150	33.79	14.8	27.80	27.8	(0.01)	17.73	17.72	(0.05)
158	38.00	17.4	31.69	31.25	(1.36)	16.62	17.75	(6.83)
167	31.96	15.2	26.80	26.23	(2.11)	16.15	17.92	(10.94)
157	23.84	13.4	19.61	19.43	(0.92)	17.72	18.48	(4.29)
148	24.24	11.8	19.94	19.84	(0.51)	17.72	18.14	(2.37)
143	23.68	11.8	19.52	19.37	(0.80)	17.55	18.20	(3.74)
Mean PE's					(1.67)			(7.40)

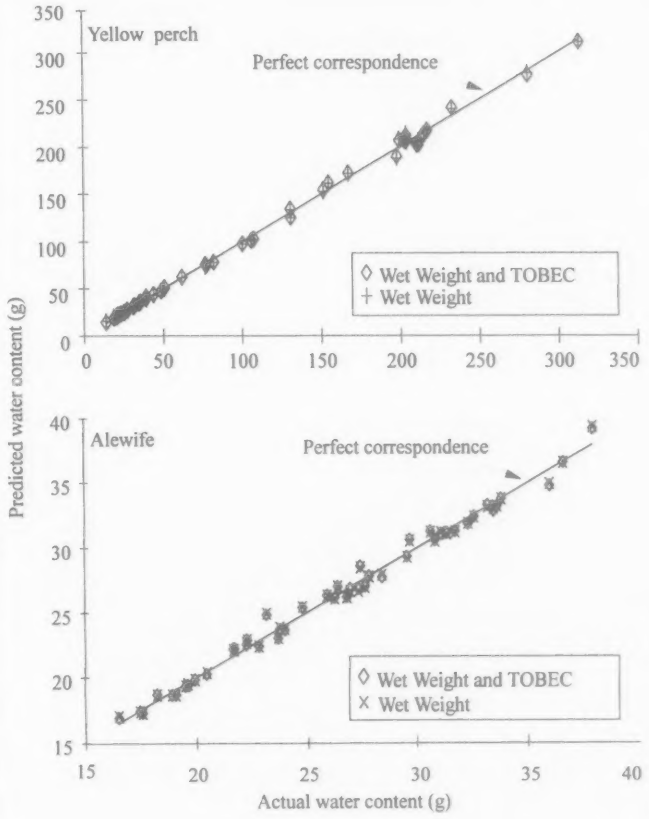

Figure 1

Comparison of the predicted and measured values of water content (g) of yellow perch and alewife. Predicted values are from multiple linear regressions with wet weight and total body electrical conductivity (TOBEC) as independent variables and from simple linear regressions with wet weight as the only independent variable.

The equation for alewife was

$$WC = -0.17206 + 0.8471 \times WWT - 0.0439 \times TOBEC \quad (r^2=0.990).$$

The slope coefficient for wet weight and the intercept in the yellow perch regression model were both significant ($P<0.01$), whereas the *TOBEC* coefficient was not ($P=0.529$). The slope coefficient for wet weight in the alewife regression was significant ($P<0.0001$), whereas both the *TOBEC* coefficient and the intercept were not ($P=0.295$ and 0.679, respectively). Both the yellow perch and alewife predictive equations provided good fit to the data for water content with mean *PE*s from all values in each data set of 3.33% and 1.67%, respectively. Wet weight, however, accounted for most of the variance within each relationship. When wet weight was used as the only independent variable in each regression model, r^2 values were both about 0.99, and were greater than the r^2 values from regressions that used only *TOBEC* as the independent variable. Predictions from these simple linear regressions (*WWT* as the only independent variable) provided nearly as good a fit to the data as the multiple linear regressions (r^2 values decreased only by about 0.00002 to 0.0005, Fig. 1).

Total length and *TOBEC* were not linearly related to water content for yellow perch. Natural log transformations for total length (Ln*TL*) and square root transformations of *TOBEC* values (sq*TOBEC*) re-

turned linear trends. When we replaced *TOBEC* with sq*TOBEC* in the regression model for yellow perch to account for nonlinearity, the r^2 value increased slightly (+0.0002) and the mean percentage error decreased (Table 1). The new yellow perch equation became

$$WC = 0.767 + 0.638 \times WWT + 0.996 \times \text{sq}TOBEC \quad (r^2=0.998).$$

Backwards stepwise multiple linear regression analysis of the yellow perch data eliminated Ln*TL* from the regression model and indicated that four other independent variables (*WWT*, sq*TOBEC*, *TL*, and an offset constant) be included. The inclusion of *TL* in the new regression model increased the r^2 value by only 0.0002, but the mean *PE* also increased to 2.56% in the new model from 2.23% in the model that included only *WWT* and sq*TOBEC*. Backwards stepwise multiple linear regression analysis of the alewife data indicated that only *WWT* was a sufficient predictor of water content in that data set.

Percentage errors in predicted values for water content were consistently larger than the mean *PE*s for *TOBEC* values ≤ 15 (<30 g yellow perch; <35 g alewife; Tables 1 and 2). Previous work indicated that the scanner is accurate for predicting lean body mass in birds down to a body weight of 20 g (Castro et. al. 1990). We found that fish sizes that returned *TOBEC* values below 10 yielded such poor results that we did not include them in our analysis (<24 g yellow perch; <16 g alewife).

Discussion

In fish, water content of the individual is strongly correlated with the whole-body wet weight and, hence, many relationships developed for the EM-SCAN use wet weight as an independent variable (Brown et al., 1993; Bai et al., 1994; Jaramillo et al., 1994). Although wet weight alone could be used to predict many of these values, assessment of the subtle differences in tissue constituents relevant to energy-balance calculations could not be accomplished. Many studies on terrestrial vertebrates have used TOBEC alone to predict tissue composition (Presta et al., 1983; Keim et al., 1988; Walsberg, 1988; Castro et al., 1990); however, all fish TOBEC studies to date have used wet weight and TOBEC as the predictor variables in regression functions. In our work, TOBEC values did not increase the predictive ability of regression functions with wet weight as the other independent variable.

Three previous studies have indicated that TOBEC can accurately predict water content in fish (Brown et al., 1993; Bai et al., 1994; Jaramillo et al., 1994). Each study indicated that TOBEC and wet weight values were correlated to body tissue constituents and water content. The inclusion of TOBEC values in regressions with wet weight as the other predictor of whole-body body water content produced slight increases in r^2 values and decreased the mean square error. We ran regression analyses with backwards stepwise elimination and found that TOBEC was eliminated from the sunshine bass data set (Brown et al., 1993) when wet weight was untransformed but was included when wet weight was $\log_e$ transformed. The regressions for sunshine bass with untransformed wet weight alone and combined with TOBEC both produced lower PEs (2.6 and 2.5 respectively) than did the Brown et al. (1993) equation with $\log_e$-transformed wet weight (PE=3.9). TOBEC was significant in regressions with wet weight for red drum (Bai et al., 1994) and channel catfish (Jaramillo et al., 1994). In these data sets, regressions, including the TOBEC variable, increased the PE from 2.2 to 3.0 for red drum (Bai et al., 1994) and decreased the PE from 4.0 to 2.7 for channel catfish (Jaramillo et al., 1994) versus the regressions with wet weight as the only independent variable. Inclusion of TOBEC values in regressions with wet weight did not substantially or consistently improve the predictions of water content over simple linear regressions with wet weight alone.

When fat is burned and replaced by water in a fish, changes in the total quantity of electrolytic salts should be reflected in TOBEC values. Hence, TOBEC values alone should be able to successfully predict water content. TOBEC values alone can predict water content values in terrestial vertebrates (r^2>0.80) and fish (r^2=0.67 to 0.988). In fish however, TOBEC predicted total wet weight equally well. If more than just test animal size affects conductivity readings, then evidence of changes in the total body content of electrolytic salts should also be apparent when TOBEC and water content values are divided by wet weight. Wet-weight–standardized TOBEC and water content values were not related for alewife, sunshine bass, or red drum (Fig. 2). The apparent trend in the yellow perch data is counterintuitive (Fig. 2) to the expected trend of increased conductance with increased water content. The strength of predictive equations for fish in the above four data sets may be solely due to effects from fish size (e.g. serum and cellular fluid volumes). The expected relationship for these parameters is apparent in our plot of the test data set from Jaramillo et al. (1994; Fig. 2). The nutrient content of diets fed to fish in those experiments was carefully controlled within groups and varied only between groups. Evidence from our study indicates some promise for using TOBEC for fish in situ-

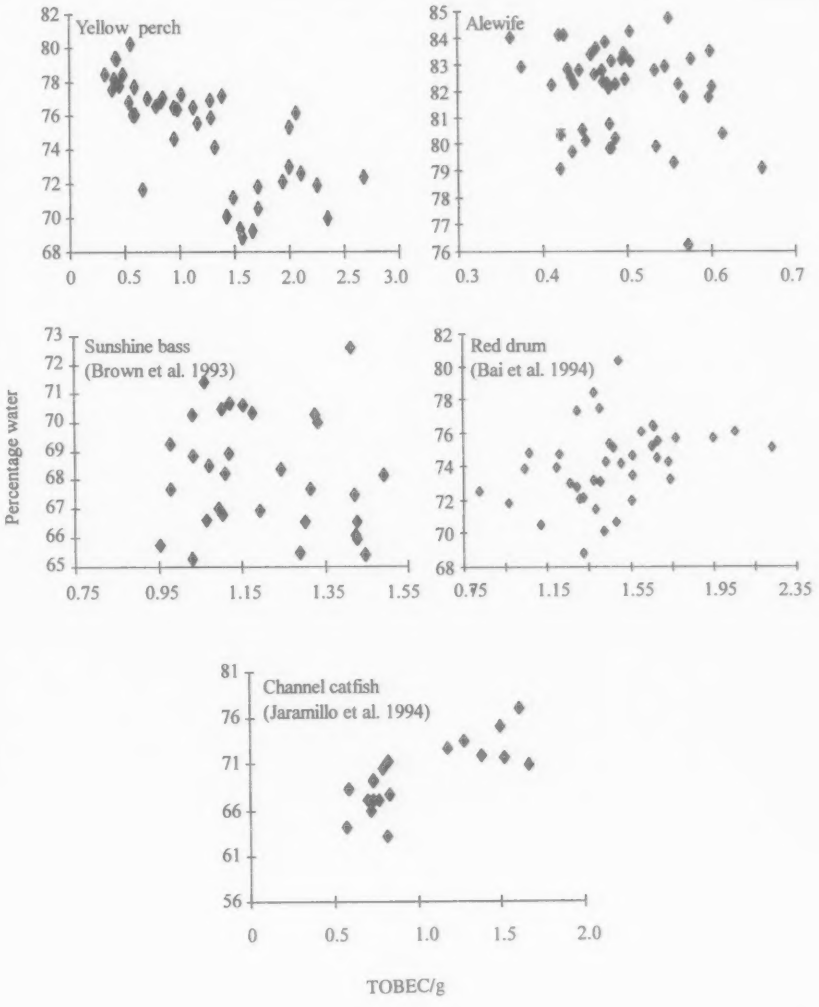

Figure 2

Comparisons between standardized values of percentage water (water content/wet weight) and total-body electrical conductivity (TOBEC/wet weight) for yellow perch, alewife, sunshine bass, red drum, and channel catfish. Data for sunshine bass, red drum, and channel catfish are from Brown et al. (1993), Bai et al. (1994), and Jaramillo et al. (1994).

ations where nutritional status can be controlled (e.g. in aquaculture) and electrolytic balance is given sufficient time to equilibrate throughout all bodily fluid (i.e. serum, cellular, and extracellular) compartments.

Our ultimate goal was to use our predictions of water content to assess the energy content of yellow perch and alewife. Our energy density relationships (Rand et al., 1994; Lantry, 1997) use percentage dry weight as the independent variable. Percentage dry weight values calculated from predicted water content did not, however, correspond to values calculated from measured water content for any of the five fish species used in TOBEC studies (Fig. 3). Our analysis indicates that further evaluations of the use of TOBEC to predict fish body composition are warranted. Fish size should be constrained to narrow ranges, and percentage water {(water content / wet weight) × 100} between individuals of different condition should be evaluated. By controlling fish size, conductivity differences due to body geometry could

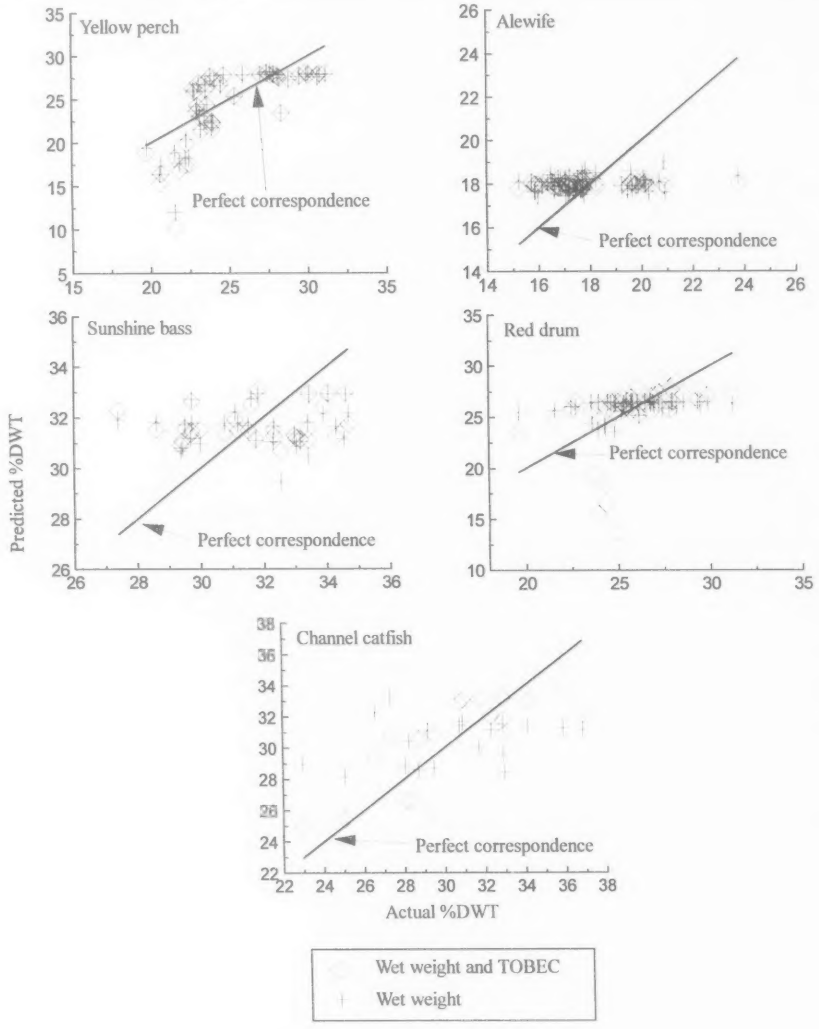

Figure 3

Comparisons between actual and predicted values of percentage dry weight (dry weight/wet weight) for yellow perch, alewife, sunshine bass, red drum, and channel catfish. Data for sunshine bass, red drum, and channel catfish are from Brown et al. (1993), Bai et al. (1994), and Jaramillo et al. (1994). The line in each panel represents the location of equivalence between actual and predicted.

be reduced and wet weight could be eliminated from prediction equations.

Variability associated with the scanning equipment, fish preparation prior to scanning, fish condition, and geometry of fish within the scanner chamber may generate errors too high to accurately predict ecologically significant changes in fish body composition. Analysis of TOBEC readings taken in fish fed, fasted, frozen, and thawed in Bai et al.'s study (1994) indicates that both physiological and physical states affect conductivity values. Dehydration in terrestial animals has also been observed to cause disproportionate changes in TOBEC values (Walsberg, 1988). Our fish were frozen in water and probably were not dehydrated; however, the death of the fish and the effect of freezing and thawing may have altered conductance. Also, the potential existed for exchange between body water and the water sur-

rounding the fish during freezing and thawing. The measurement of TOBEC values, however, did not produce consistent improvement in the predictability of whole-body water content in fish from any of the five data sets considered. This analysis indicates that TOBEC procedures will not be able to predict with sufficient accuracy the water content of fish sampled from field situations and frozen in water for later analysis.

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Abstract.—We measured age and growth of larval striped bass (*Morone saxatilis*) and white perch (*M. americana*) and tested whether growth and survival were enhanced in relation to a seasonal pulse ("bloom") of high zooplankton abundance. Growth rates were lowest before the zooplankton bloom and highest afterwards for both fish species. An index of recruitment potential (instantaneous growth rate, G, divided by instantaneous mortality rate, Z) did not relate clearly to either water temperature or to zooplankton abundance in the case of striped bass but did relate to both factors for white perch. Retrospective analysis of hatch dates in recruited juvenile striped bass from the same year class indicated that later, faster growing cohorts were under-represented when compared to the larval cohort distribution, and that cohorts that co-occurred with high densities of the cladoceran zooplankton *Bosmina freyi* were over-represented. Comparison of these results with similar analyses from other systems suggests that biotic controls on year-class strength may predominate in estuarine systems where physical factors are relatively damped (Hudson) but may play relatively minor roles in those systems with high physical variability.

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Growth, mortality, and recruitment of larval *Morone* spp. in relation to food availability and temperature in the Hudson River

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Survival during the first year of life determines the year-class strength of many fish. The degree to which biotic or physical factors regulate recruitment of fish from larval to juvenile stages varies from one aquatic system to another, and even temporally within systems (Leggett and DeBlois, 1994). The factors promoting or inhibiting recruitment are a subject of intense interest both in theoretical analysis and practical management of fish populations (cf. Hilborn and Walters, 1992). Mortality of young fish below harvestable size is difficult to observe and difficult to measure by means of standard approaches to population assessment (e.g. mark and recapture).

The age and growth rates of young fish, however, can be precisely quantified with otolith analysis (cf. Campana and Neilson, 1985; Secor et al., 1995). This technique has permitted the determination of hatching dates, age, and growth rates of both larvae and juveniles of many species. Comparisons of hatching dates and growth between life stages (e.g. larvae vs. juveniles) allow inferences about the fates of larvae. For example, if larval survival is particularly high during a specific time period, analysis of juvenile hatch dates should reflect the differential survival (assuming adequate sampling). These measures can also be used with repeated samplings of the population to track the growth and mortality of specific age classes (e.g. weekly cohorts) over time. Relationships between these cohort-based rates can be analyzed with respect to variables such as food availability, predation, and the physicochemical environment.

We previously documented that larval striped bass (*Morone saxatilis*) and white perch (*M. americana*), which co-occurred with increases in crustacean zooplankton in the tidal Hudson River, showed a potential energetic advantage compared with larvae that preceded the zooplankton increase (Limburg et al., 1997). A major increase ("bloom") in zooplankton in early summer is a key feature of the Hudson estuary. Larvae occurring before the bloom are exposed to sparse zooplankton densities and low temperature, both of which are associated with mortality risks (Rogers and Westin, 1981; Chesney, 1989; Margulies, 1989; Uphoff, 1989; Tsai, 1991; Cowan et al., 1993). Larvae occurring during and after the bloom have high consump-

tion rates and are at lower risk of exposure to suboptimal or lethal temperatures.

Do these temperature and food conditions translate into differential survival conditions for larval *Morone* spp. in the Hudson River? We addressed this question using methods of otolith age and growth-rate reconstruction. Specifically, we tested if periods of high food availability (zooplankton bloom conditions) were also periods of high larval growth rates. Further, by analyzing the otoliths of juveniles of the same year class (i.e. successful recruits from the larval stage), we also assessed whether or not fish that survived the larval period had high larval growth rates and hatching dates associated with the zooplankton bloom.

Studies of *Morone saxatilis* in Chesapeake Bay tributaries have used both interannual variations in larval abundance (Uphoff, 1989) and cohort analysis methods (Rutherford and Houde, 1995; Secor and Houde, 1995; Rutherford et al., 1997) to establish that rapid drops in water temperature below 12°C virtually eliminate larval cohorts. These studies concluded that the frequency of low temperature events can be an important factor in the recruitment of striped bass in those systems. In contrast, Pace et al. (1993) found no evidence that temperature affected interannual variation of *Morone* spp. recruitment in the Hudson River, although Dey (1981) presented evidence for temperature-induced mortality in Hudson River striped bass in 1976 (temperature dropped suddenly from 15° to 12°C in late May). Thus temperature effects, although not detectable among years, might still manifest themselves as seasonal variability. In this paper we examine the 1994 year classes of striped bass and white perch, including an appraisal of the relation of zooplankton abundance and temperature to growth and mortality of individual cohorts. With this information, we can make tentative comparisons between analyses for the Hudson River and Chesapeake Bay.

Materials and methods

The Hudson River, a partially stratified estuarine-river system in New York State, is tidal up to the Green Island dam, 245 river kilometers (rkm) from the mouth. All life stages of white perch are found throughout the oligohaline and freshwater sections of the estuary (Klauda et al., 1988). Striped bass adults migrate into the estuary in spring to spawn. Larvae are found in both freshwater and oligohaline sections (Boreman and Klauda, 1988). Juveniles spread throughout the estuary and move seaward during late summer and fall (Dovel, 1992).

Larval collections and preparation

Field collections of larval *Morone* spp. were undertaken in the spring and early summer of 1994. Sampling details are described in Limburg et al. (1997). Briefly, three sites, in the upper (Kingston, rkm 148), middle (New Hamburg, rkm 105), and lower (Haverstraw Bay, rkm 65–70) portions of the estuary were sampled between 18 May and 6 July; all sites overlapped with spawning areas. Sampling frequency was designed to examine larval and zooplankton dynamics before, during, and after the intensive bloom of the cladoceran zooplankton *Bosmina freyi* (=*Bosmina longirostris* with older nomenclature). Fish were collected during the daytime with 5-min oblique tows of 0.5-m diameter bongo nets (500-mm mesh). Five replicate tows were conducted at each site on each date. Samples were preserved in 100% ethanol which, when diluted with the sample, reached a final concentration of no less than 75%. Care was taken not to over-dilute the samples below this concentration because of risk of otolith erosion (Brothers, 1987).

In the laboratory, fish were sorted by family and stored in fresh 100% ethanol. Three replicates were chosen at random from the five available at individual stations for each sampling date, and up to twenty *Morone* individuals were arbitrarily selected from each replicate; more replicates were used when larval abundances were low. The larvae were rehydrated, soaked for 15 min in sodium borate buffer solution (30% saturated sodium borate), and then cleared by adding a small quantity of trypsin to the buffer solution. *Morone* larvae were measured to 0.1 mm notochord length (NL) and identified to species by a combination of internal and external characters (Limburg et al., 1997). Lengths were not corrected for preservation shrinkage, but rehydration and clearing fully relaxed constricted musculature so that lengths were readily measured. Otoliths were visible under 25× magnification on a stereomicroscope. Fine insect pins, the tips of which were sharpened further, were used to dissect the sagittal otoliths. Otoliths of fish less than 5 mm NL were cleaned in deionized water and placed directly in mineral oil for later viewing. Following the suggestion of Rutherford (1992), otoliths of larger (>5 mm NL) fish were embedded in Spurr's epoxy, then ground and polished with a series of increasingly fine grinding papers (down to 3 mm).

Juvenile fish collection and preparation

In order to make comparisons between recruited juveniles and larvae, we obtained a total of 218 juve-

nile striped bass from five sites along the Hudson River (at river kilometers (rkm) 40, 63, 95, 114, and 201) during July (n=37), August (n=88), and September (n=93) from state-run fishery surveys. Fish were collected either with a 30.5-m (100-ft) beach seine with 6.1-m bag, 0.64-cm mesh, or with a 61-m (200-ft) beach seine with 1.27-cm stretch mesh (0.64 cm square). Fish were held on ice in the field, then stored frozen.

In the laboratory, juvenile striped bass were defrosted, and standard, fork, and total lengths (SL, FL, and TL respectively) were measured. Sagittal otoliths were removed from each fish, cleaned in 10% sodium hypochlorite (bleach), and embedded in Spurr's epoxy. One otolith from each pair was subsequently sectioned along the transverse axis and prepared in thin section according to the method of Secor et al. (1991). A total of 63 juvenile otoliths were successfully prepared and read.

Otolith microstructure analysis

Otolith microstructure was examined with a light microscope with a video attachment connected to an image analysis system. Specimens were viewed in the sagittal plane by using the digital image for projection. Most specimens were viewed at magnifications of 500–750×, but 1250× (100× objective) was used to resolve the finest increments. Increments were counted several times and averaged. Larval otoliths were examined by one reader, and two independent readers were used to cross-check the consistency of increment counts for juvenile striped bass otoliths.

Ages were estimated by correcting for the effect of temperature on the timing of first increment deposition (Houde and Morin[1]). Age at first increment deposition was estimated as (11.56–0.45 T) for striped bass and (9.05–0.32T) for white perch, where T is water temperature (Houde and Morin[1]). From our measurements of water temperature (n=30) from 14 April to 19 July 1994, we estimated a linear increase in river temperatures over the study period with the regression

$$Water\ temperature = -17.6 + 0.23 \times (day\ of\ year) \quad [r^2=0.98,\ P<10^{-4}].$$

We used this equation to estimate water temperatures on the day of the first increment and assumed little change in temperature back to the hatching day. Ages were estimated as number of increments + temperature adjustment; hatching dates were then backcalculated from the date of capture.

Image analysis was used to measure increment widths. For larvae, widths of the total number of increments on an otolith were measured and averaged to obtain an average daily increment width (in mm). In addition, when possible, widths of the first five increments (I1–I5) and of the sixth and seventh increments (I6–I7) were measured to obtain two standardized estimates of early growth. Increments I1–I5 exhibited slower average growth than did increments I6–I7. In all, otoliths of 248 larval striped bass and 526 larval white perch were examined.

Somatic growth rates were calculated for larvae and juveniles by the equation

$$(L_t - L_{t_0})/Age,$$

where L_t = length at capture; and
L_{t_0} = length at hatch.

L_{t_0} is assumed to be 3.0 mm for white perch and 4.0 mm for striped bass (Mansueti, 1958; Lippson and Moran, 1974). In addition, "standardized" growth rates were calculated for 7-day-old larvae so that comparisons of growth could be made before, during, and after the zooplankton bloom. This was done by determining the number of increments deposited by age 7 (typically <5), multiplying that number by the mean increment width of I1–I5, adding the result to the otolith core radius, and then by using the following regressions to calculate standard lengths at age 7 days:

$$SL_{SB} = -0.37 + 1.95\ (\text{natural log of otolith width}) \quad [r^2= 0.83,\ n=210,\ P<10^{-4}],$$

$$SL_{WP} = -1.67 + 2.18\ (\text{natural log of otolith width}) \quad [r^2= 0.88,\ n=522,\ P<10^{-4}].$$

The same procedure was used to backcalculate age 7-d somatic growth rates for juvenile striped bass.

Mortality and recruitment potential

For purposes of comparison with Chesapeake Bay studies, mortality rates were estimated for fish larvae collected at New Hamburg (rkm 105) by using a method similar to that described in Secor and Houde (1995). Cohort analyses were confined to the New Hamburg station because we were able to collect both species consistently in large numbers. All larvae in these samples were counted, and lengths of at least

[1] Houde, E. D., and L. G. Morin. 1990. Temperature effects on otolith daily increment deposition in striped bass and white perch larvae. International Council for the Exploration of the Sea, Copenhagen, Denmark, Council Meeting 1990/M:5.

100 individuals were measured unless fewer than 100 occurred in the sample. Densities (numbers of fish per 1000 m^3) by 0.5-mm size class were computed and corrected for differences in day and night catch efficiencies, and for extrusion of smallest individuals, by using regressions in Houde et al.[2]

Age distributions of fish collected on different sampling dates were estimated from the otolith-aged fish. Rather than estimate variance from an age–length regression and use it to assign probabilities of age-at-length (Secor and Houde, 1995), we estimated the mean and variance in ages for each 0.5-mm size group and used those parameters to assign age-at-length probabilities (z-scores).

The corrected catch densities, separated into 0.5-mm size classes, were multiplied by the appropriate size-based age distributions to obtain numbers of fish of different ages. Following Secor and Houde (1995), hatching dates were calculated and fish were grouped into 6-d cohorts. In some of the cohorts, the age-estimation technique resulted in very small initial numbers of fish. If these numbers were tenfold smaller than the maximum calculated densities of a cohort, they were deleted from the data set. Then mortality rates (Z) of the cohorts were estimated by fitting an exponential decay model to abundances of fish within specific cohorts over time.

We used an index (Rutherford and Houde, 1995; Secor and Houde, 1995) of mean instantaneous growth (estimated for an individual fish as $G = \ln(W_t/W_0)/t$, where t = age at capture, W_t = weight at capture, and W_0 = weight at hatch) over instantaneous mortality rate (G/Z) to compare the benefits accrued in growth versus the costs expressed as mortality for larvae occurring before, during, and after the zooplankton bloom. Weights were estimated from lengths by the equation

$$W = 3.763 \times 10^{-4} \times L^{(4.2879)} \quad [n=67,\ r^2=0.92,\ P<10^{-6}];$$

where W = mg wet weight; and
L = length in mm (Limburg et al., 1997).

Finally, we estimated the dates of first-feeding for striped bass larvae and juveniles with respect to the zooplankton bloom. We assumed that fish begin to feed at day 5 after hatching. We used an age-length regression from the 63 juvenile striped bass to estimate ages of the remaining juveniles. We assumed that little or no out-migration would be occurring in July and August (Dovel, 1992), so that fish collected during these months would show the effect of differential recruitment without the confounding process of out-migration.

Table 1

Mean (± SD) somatic growth rates (GR, mm/d) of larval white perch and striped bass, by site and date, 1994. (n=526 white perch and 248 striped bass; n.d.=no data; — = zero fish in samples.)

	White perch			Striped bass		
Date	Mean GR	SD	n	Mean GR	SD	n
Haverstraw Bay (rkm 65–70)						
18 May	0.181	0.067	15	0.072	0.069	9
24 May	—	—	0	—	—	0
3 June	0.186	0.054	17	0.185	0.111	29
7 June	0.409	0.215	9	0.286	0.128	25
10 June	0.211	0.086	8	0.178	0.111	8
13 June	0.382	—	1	0.250	0.046	17
22 June	0.427	0.199	3	0.293	0.088	36
29 June	0.313	—	1	0.284	0.007	3
6 July	n.d.			n.d.		
New Hamburg (rkm 105)						
18 May	—		0	—		0
24 May	0.155	0.037	37	0.069	0.022	3
3 June	0.192	0.060	47	0.162	0.127	11
7 June	0.218	0.070	42	0.216	0.084	14
10 June	0.236	0.085	35	0.247	0.030	4
13 June	0.210	0.081	29	0.224	0.039	8
22 June	0.265	0.083	11	0.207	0.056	9
29 June	0.306	0.049	11	0.252	0.084	20
6 July	0.331	0.052	9	0.264	0.062	40
Kingston (rkm 148)						
18 May	—		0	—		0
24 May	0.205	0.061	9	0.044	0.027	3
3 June	0.167	0.053	52	0.032	0.054	6
7 June	0.200	0.053	47	0.146	0.189	2
10 June	0.201	0.089	59	0.017	—	1
13 June	0.196	0.086	35	—	—	0
22 June	0.245	0.113	12	—	—	0
29 June	0.300	0.099	37	—	—	0
6 July	n.d.			n.d.		

Results

Growth rates

Mean somatic growth rates (GRs) of both species of *Morone* tended to be lowest prior to the bloom (before 3 June); rates were higher after the bloom (22 June and later), especially for white perch (Table 1;

[2] Houde, E. D., E. J. Chesney, R. M. Nyman, and E. S. Rutherford. 1988. Mortality, growth and growth rate variability of striped bass larvae in Chesapeake subestuaries. Interim Report to Maryland Department of Natural Resources. Chesapeake Biological Laboratory, Solomons, MD. Ref. No. [UMCEES]CBL 88-96, 126 p. [Available: Chesapeake Biological Laboratory, Box 38, Solomons, MD 20688.]

Fig. 1). There were significant site, species, and site × species effects on mean somatic GRs ($P<10^{-4}$), with highest GRs at the southernmost site (Haverstraw Bay). Mean somatic growth rate for striped bass was 0.053, 0.232, and 0.238 mm/d at Kingston, New Hamburg, and Haverstraw Bay, respectively (greater than an eightfold difference between highest and lowest; it should be noted that the total number of fish sampled at Kingston was very small). Growth rates for white perch did not vary as greatly but did vary in the same longitudinal direction (0.209, 0.215, and 0.245 mm/d at Kingston, New Hamburg, and Haverstraw Bay). Time series of somatic GRs, averaged over all sites for each species (Fig. 1), revealed species-specific patterns of growth with respect to the zooplankton bloom period. Striped bass GRs accelerated more strongly during the bloom period than did GRs of white perch.

Somatic growth rates were related to water temperature as

$$GR = -0.050 + 0.013 \times MWT \quad [r^2=0.15,\ n=774,\ P<10^{-6}],$$

where MWT = mean water temperature during the life of the individual larva (calculated as the temperature midway through the larva's life).

The effect of temperature was removed by calculating residuals of this regression and by using the residuals as a new data set (temperature-adjusted GRs) to assess growth relative to zooplankton dynamics. Temperature-adjusted somatic GRs for white perch showed little trend with respect to the zooplankton bloom, whereas striped bass GRs peaked during the bloom (Fig. 2). This peak was not significantly greater than the adjusted GRs after the bloom, but both differed significantly from the prebloom-adjusted GRs.

Our comparisons of somatic growth rates are based on fish larvae of different sizes and ages. Comparisons of growth rates for a standardized age (we chose age=7 days) can eliminate this potential source of bias. Mean 7-d GRs (Fig. 3) showed a pattern similar to that for overall mean GR, indicating that growth rates did not peak during the zooplankton bloom. Although both species' 7-d GRs varied significantly with respect to the bloom (with highest GRs after the bloom), white perch 7-d GRs did not differ significantly from striped bass 7-d GRs.

Recruitment potential at New Hamburg

Ten 6-d age cohorts, grouped arbitrarily starting 1 May (cohort A) and extending through the period beginning 24 June (cohort J), were identified in the catches at New Hamburg (rkm 105). Insufficient numbers prohibited estimation of Z for the last striped bass cohort (J, 24–29 June) and the last two white perch cohorts (I and J). Estimates of white perch starting densities (natural log of N_0) were highest in early cohorts (A and B; Table 2). Striped bass initial density estimates were highest in later cohorts (E, G, and H; Table 2). Earliest and latest cohorts were poorly estimated owing to low sample numbers.

Estimated mortality rates were highest in cohort A for both species (Table 2). Cohort A (period starting 1 May) appeared only in two samples; presumably recruitment from this group was very low. For white perch, mortality rates declined more or less monotonically with time (and therefore also with increasing temperature). Striped bass mortality rates were also lowest in the latest cohorts, but there did not appear to be a systematic decline (Table 2).

Instantaneous growth rates (G) in striped bass did not vary

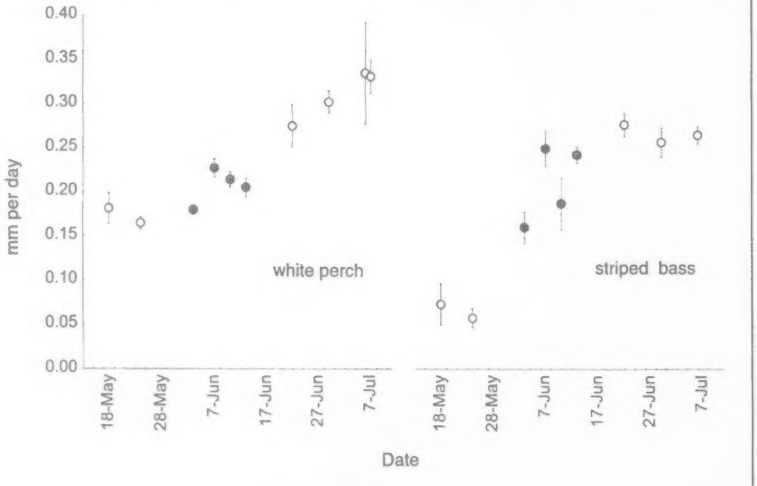

Figure 1

Mean (±SE) somatic growth rates of larval white perch and striped bass, averaged across all sampling sites, 18 May–6 July 1994. The darkened points on each graph indicate the period of the *Bosmina* bloom.

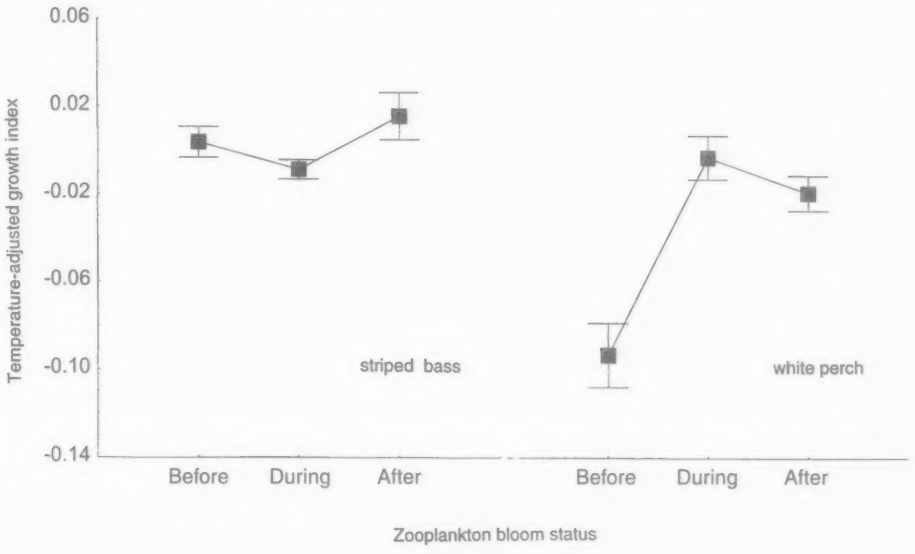

Figure 2

Mean (±SE) somatic growth rates (residuals) of larval white perch and striped bass with the effect of temperature removed, grouped with respect to the *Bosmina* bloom.

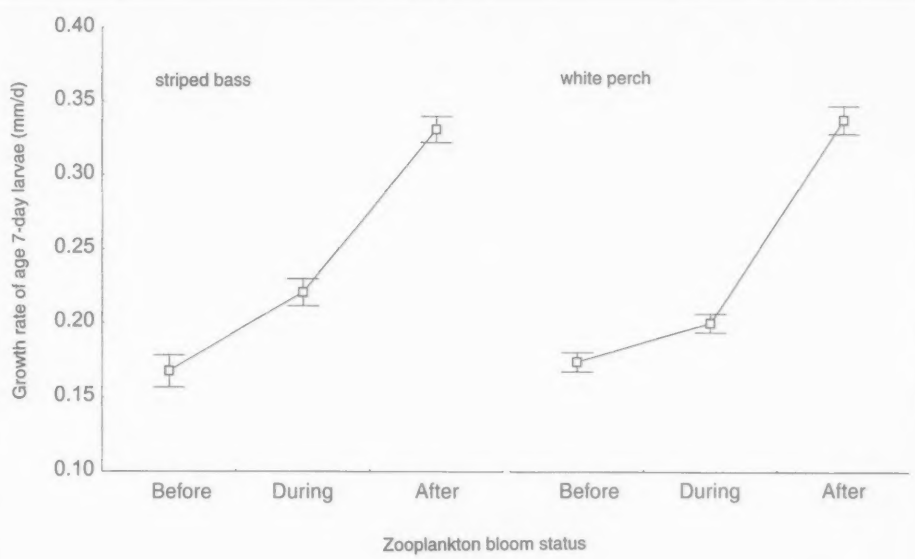

Figure 3

Mean (±SE) growth rates of 7-day old larval white perch and striped bass, grouped with respect to the *Bosmina* bloom.

in a consistent manner, either with temperature or zooplankton density (Table 3). Striped bass *G* peaked in cohort E (those hatched 25–30 May), as did *G*/*Z*. Neither *G*, *Z*, nor *G*/*Z* for striped bass were significantly affected by either temperature or zooplankton densities estimated during the week of hatching.

Table 2

Estimates of natural logs of initial densities (N_0, numbers per 1000 m^3) and mortality rates (Z) for 6-d cohorts of striped bass and white perch in the Hudson River (New Hamburg site). Letters designate cohorts referred to in text.

Date	Cohort	$\ln(N_0)$	SE	Z	SE	r^2	P	n
Striped bass								
1–6 May	A	4.132		1.51				2
7–12 May	B	7.598	6.153	0.262	0.315	0.41	0.55	3
13–18 May	C	6.919	2.070	0.263	0.132	0.66	0.19	4
18–24 May	D	5.941	2.207	0.296	0.110	0.64	0.05	6
25–30 May	E	7.690	0.751	0.260	0.034	0.94	0.001	6
31 May–5 June	F	6.502	0.549	0.176	0.027	0.91	0.002	6
6–11 June	G	8.808	0.103	0.221	0.005	0.99	0.01	3
12–17 June	H	7.645	0.767	0.163	0.048	0.92	0.18	3
18–23 June	I	6.977		0.145				2
White perch								
1–6 May	A	16.653		0.785				2
7–12 May	B	12.484	2.905	0.509	0.138	0.87	0.07	4
13–18 May	C	9.221	1.299	0.328	0.064	0.87	0.007	6
18–24 May	D	8.058	1.284	0.241	0.064	0.78	0.02	6
25–30 May	E	9.682	1.022	0.304	0.051	0.90	0.004	6
31 May–5 June	F	7.861	0.807	0.187	0.049	0.83	0.03	5
6–11 June	G	5.811	1.295	0.044	0.087	0.21	0.70	3
12–17 June	H	7.885		0.137				2
18–23 June	I	insufficient data						

Table 3

Estimated instantaneous growth (G) rates (± standard error), and index of recruitment potential (G/Z) for 6-d cohorts of larval striped bass (SB) and white perch (WP), New Hamburg (rkm 105), 1994. Calculated water temperatures (see "Methods") and zooplankton densities (copepods and *Bosmina*, no./L), corresponding to each cohort, are included. Zooplankton densities are offset by 5–7 d from actual sample dates (e.g. the zooplankton sample associated with cohort G was collected on 10 June) to approximate the lag in initial feeding by larvae. n.d. = no data. G/Z in parentheses were calculated with the previous cohorts' Z estimates but were not used in analyses.

Cohorts	Dates	Temperature (°C)	Zooplankton density	G_{SB}	SE	G/Z_{SB}	G_{WP}	SE	G/Z_{WP}
A	30 Apr 1994								
B	5 May 1994	12.2	n.d.				0.125	0.006	0.245
C	12 May 1994	13.6	1.88	0.205	0.056	0.779	0.125	0.006	0.380
D	18 May 1994	15.0	10.9	0.205	0.056	0.693	0.141	0.043	0.583
E	24 May 1994	16.4	35	0.564	—	2.169	0.132	0.010	0.436
F	30 May 1994	18.0	80.5	0.070	0.009	0.398	0.159	0.007	0.850
G	05 Jun 1994	19.4	520	0.092	0.012	0.416	0.378	—	8.521
H	11 Jun 1994	20.8	70	0.113	0.021	0.693	0.196	—	1.427
I	17 Jun 1994	22.2	4.1	0.097	0.035	0.671	0.150	0.036	(1.095)
J	23 Jun 1994	23.5	5.6	0.171	0.228	(1.179)			

In contrast, white perch G was significantly correlated with zooplankton density ($G_{WP}=0.136+4.64\times10^{-4}\times(\textit{zooplankton density})$, $r^2=0.96$, $P<10^{-4}$). The high significance was due to the highest growth at a time of maximum zooplankton density (520 individuals/L), but the regression relationship remained the same even with removal of the influential point. Lowest mean G/Z occurred before the bloom (0.35 ±0.18 SD, $n=4$), intermediate G/Z during the bloom (1.27 ±1.06, $n=2$) and highest afterward (2.53 ±2.04, $n=2$), but these were not significantly different. Although there is a tendency toward increasing G/Z with time (and temperature), it was not statistically significant either.

Table 4

Mean growth (mm/d, calculated from otoliths) at age 7 d after hatching of larval and juvenile striped bass, 1994.

	Bloom status	Mean	SD	*n*
Larvae	Before	0.167	0.072	45
	During	0.221	0.062	47
	After	0.331	0.079	77
Juveniles	Before	0.199	0.080	18
	During	0.215	0.063	33
	After	0.223	0.056	12

Retrospective early life histories of juvenile versus larval striped bass

Larval and juvenile striped bass from the 1994 year class had similar patterns of early growth, as measured by mean growth (mm/d) through age 7 days after hatching. In both groups, growth rates increased monotonically from May through early July corresponding with before, during, and after the zooplankton bloom ($P<0.01$; Table 4). Juvenile mean growth rates before and during the zooplankton bloom were higher (though not significantly so) than larval growth rates in the corresponding periods. However, mean 7-d growth rates of postbloom juveniles were significantly ($F(1,87)=21.03, P<10^{-4}$) lower than growth rates of postbloom larvae.

The frequency (distribution of hatching dates) of juvenile striped bass born in the 6-d cohorts beginning 1 May did not correlate well with the index of recruitment (*G/Z*) developed from the larval data (*Frequency*=0.118+0.021 (*G/Z*), $r^2=0.03$).

Because of our ability to "hind-cast" the distribution of hatching dates of juveniles and larvae, we estimated the relative proportions of both larvae and juvenile striped bass that would have begun to feed during the zooplankton bloom (assuming that feeding begins at day 5 after hatching). For this analysis, we analyzed the fish response to *Bosmina* and copepods. For *Bosmina* we assumed that fish with hatching dates between 29 May and 8 June would be able to feed on *Bosmina*; we further assumed that fish hatched between 5 June and 17 June would also be able to take advantage of the bloom of copepods (note that in this analysis we assume that *Bosmina*-feeders occurred above Haverstraw Bay and that copepod feeders occurred throughout the river).

Larval distributions indicated that 37% of the population began to feed after the bloom of *Bosmina* (Fig. 4A), and 26% initiated feeding during the bloom. Of larvae that occurred in the geographic range of *Bosmina* (at New Hamburg and Kingston), over half began to feed after the bloom and less than 20% began feeding during the bloom. In contrast, 44% of juvenile striped bass began to feed during the bloom of *Bosmina* (Fig. 4A); and of the fish identified as first feeding prior to the onset of the bloom, 23% were hatched after 25 May, so that these fish would have been relatively close to first feeding at the time that *Bosmina* numbers increased exponentially. Those survivors to the juvenile stage that began to feed after the *Bosmina* bloom composed the smallest fraction (26%). The first-feeding distributions of larvae and juveniles differed significantly with respect to the *Bosmina* bloom (2×3 contingency analysis, $\chi^2=13.4$, df=2, $P<0.01$), whereas distributions of larvae and juvenile fish with respect to the bloom of copepods did not differ from one another ($\chi^2=3.7$; Fig. 4B). Thus the time period associated with the *Bosmina* bloom, and not the copepod bloom, appears to have been related to successful striped bass recruitment.

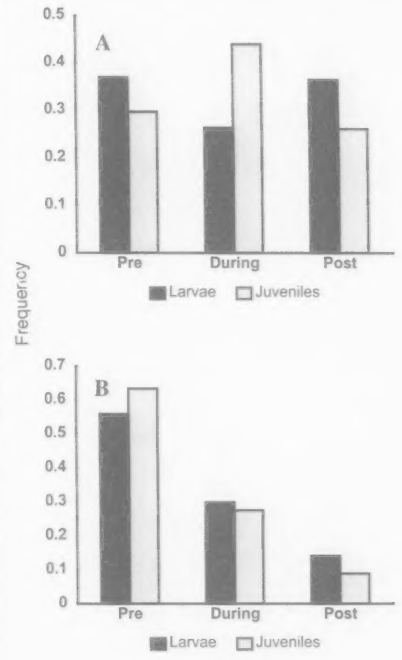

Figure 4

Fraction of larval (black bars) and juvenile (gray bars) 1994 striped bass populations that were estimated to be feeding before, during, and after blooms of (**A**) *Bosmina freyi* and (**B**) copepods in the Hudson River.

Discussion

Evidence from this study provides some support for the relation between larval growth rates and tem-

perature found by Rutherford and Houde (1995) for the Potomac River and Upper Chesapeake Bay and by Secor and Houde (1995) for striped bass larvae in the Patuxent River. However, the relationship we found was weak (r^2 only 0.15). Some measures of growth were also enhanced with increased food availability. Because of the similarity of our approach with that of these previous Chesapeake researchers, we can compare the fates of striped bass larvae in the Chesapeake and Hudson systems.

Temperatures during the larval period were more variable in the Chesapeake tributaries in the studies referred to above than in the Hudson in 1994. In the Patuxent in 1991, water temperatures in April (when nearly 90% of eggs were produced) fluctuated erratically between approximately 13° and 20°C. In May, temperatures rose through the month from 20° to 29°C (Secor and Houde, 1995). In the Potomac (1987–89) and Upper Bay (1988–89) (Rutherford and Houde, 1995), water temperatures also fluctuated, dropping in 1989 during one event from above 16°C to around 12°C, the lower lethal limit for striped bass larvae (Morgan et al., 1981). April and May water temperatures in the Nanticoke, another Chesapeake tributary, also fluctuated in 1992 and 1993 (Kellogg et al.[3]). In contrast, 1994 water temperatures in the Hudson River increased linearly from mid-April through mid-July with little fluctuation.

In spite of the overall warmer temperatures, calculated instantaneous growth rates of larval striped bass grouped into 6-d cohorts were lower in the Patuxent River (mean instantaneous G=0.126/d, range 0.11–0.14) than in the Hudson (mean G=0.190/d, range 0.070–0.564). Nanticoke River growth rates were intermediate (0.166 in 1992, 0.159 in 1993; Kellogg et al.[3]). Hudson striped bass larvae grew at rates similar to those for Potomac River (0.208 and 0.181/d for 1987 and 1989) and Upper Chesapeake Bay larvae (0.183/d). In terms of growth in length, both moronid species in the Hudson grew faster than Patuxent River striped bass larvae (Hudson white perch=0.212 mm/d ±0.101 SD, Hudson striped bass=0.218 mm/d ±0.121 SD, Patuxent striped bass=0.17 mm/d for 0–25 d). Note that Dey (1981) estimated Hudson River striped bass larval growth rates (in 1973–76) as ranging from 0.1 to 0.2 mm/d, based on analysis of weekly changes in mean lengths of larvae. Growth rates in the present study are higher than Dey's estimate and fall within the range of the Potomac (mean growth rates 0.18–0.26 mm/d, 1987–89; Rutherford and Houde, 1995). Differences in growth rates are likely due to a combination of factors in any given year and site; unfortunately, multiyear studies of larval growth rates, which would provide ranges of variation, are few.

An index of population growth, G/Z, has been used as an index of striped bass recruitment success (Rutherford and Houde, 1995, Secor and Houde, 1995, Rutherford et al., 1997, Kellogg et al.[3]) in Chesapeake tributaries because the index corresponded, at least on a seasonal basis, with production of 8-mm larvae, which is, in turn, correlated with year-class strength in the Chesapeake system. The G/Z did not correlate well with our index of recruitment, i.e. juvenile striped bass recruits. We did not examine juvenile recruitment of white perch, nor are we aware of any otolith-based studies of white perch recruitment in other ecosystems.

The G/Z method as applied at New Hamburg must be viewed cautiously, as calculations of mortality (Z) for individual cohorts are based on a few samples and are not well constrained (hence the large standard errors for some cohorts, Table 2). Further, although in aggregate a large number of individuals were examined in this study, growth rates for individual cohorts were estimated from a limited sample size. Finally, there is likely a substantial variability in time and space for both G and Z that currently exceeds measurement capacity even in the most diligent field study. Given these issues of accuracy and precision, our analyses should indicate general trends, but they cannot yet be viewed as conclusive.

In both the Chesapeake Bay and Hudson River, it appears that lowest mortality rates in striped bass larvae fall within a constrained temperature range. Secor and Houde (1995) found a convex parabolic relationship of Patuxent striped bass mortality rates with temperature; minimum mortality rates were associated with cohorts that experienced water temperatures of 16–18°C in the first 25 days of life. Rutherford and Houde (1995) did not find so neat a relationship but rather noted that low mortality rates occurred in early May cohorts of Potomac striped bass larvae, which coincided with water temperatures around 16°C. Mortality rates of Hudson River striped bass in 1994 were also lowest in cohorts associated with water temperatures of 16.4° to 18.0°C during the week of hatching (31 May to 5 June, Table 2); however, first feeding by these cohorts also coincided with the zooplankton blooms. White perch mortality rates appeared to decline with increasing temperature.

[3] Kellogg, L. L., E. D. Houde, and D. H. Secor. 1996. Egg production and environmental factors influencing larval population dynamics in the Nanticoke River, 1992–1993. Chapter 1 *in* E. D. Houde and D. H. Secor (eds.), Episodic water quality events and striped bass recruitment: larval mark-recapture experiments in the Nanticoke River. Final Rep. to Maryland Dep. Natural Resources, Chesapeake Bay Research and Monitoring Division. University of Maryland, Ref. No. [UMCEES]CBL 96-083. [Available: Chesapeake Biological Laboratory, Box 38, Solomons, MD 20688.]

In the Chesapeake system, temperature can play a key role in setting year-class strength for striped bass (Rutherford and Houde, 1995; Secor and Houde, 1995), although it is not always the determining factor (e.g. Kellogg et al.[3]). Complete failures of individual cohorts were associated with rapid temperature drops down to 12°C (Rutherford and Houde, 1995). Dey (1981) hypothesized that early cohorts of Hudson River striped bass were eliminated by a sudden drop in water temperatures in late May 1976, and simulation analysis by Boreman (1983) supported this inference.

Nevertheless, there was no relationship between temperature and year-class strength for Hudson River moronids over the period 1974–90 (Pace et al., 1993). Examining a 40-yr record of Hudson River temperatures, we found that the likelihood of lethal low temperature events (defined as ≤12°C) declines rapidly during the latter half of April (Fig. 5). Early spawned cohorts of both moronid species have a risk for low-temperature mortality events, but most cohorts are spawned after early May and are highly unlikely to experience this direct source of mortality (Fig. 5).

We have demonstrated that, like Chesapeake striped bass growth rates, larval moronid growth rates are linked (albeit weakly) to temperature in the Hudson River. Nevertheless, differential mortality occurred on the faster-growing, late cohorts of striped bass. We postulate that this mortality was due to predation. Secor and Houde (1995) also speculated that increased mortality rates observed in late Patuxent cohorts was due to predation. Hudson River moronid larvae that co-occurred with the zooplankton blooms were able to benefit energetically from increased food availability in relation to prebloom conditions (Limburg et al., 1997). Consumption rates continued to be high after the bloom, however, so that energetically the larvae continued to do well. Warmer temperatures after the bloom would have enabled larvae to swim faster and encounter more prey, but they would also potentially have encountered more predators. Thus, we infer that late cohorts suffered differentially greater predation.

We suggest that larger estuarine nurseries, such as the Hudson River, provide more damping of physical fluctuations in characteristics such as water temperature than do smaller estuaries with "flashier" drainage regimes. If this is the case, we might expect Chesapeake Bay moronid stocks to be more at risk for episodic, density-independent mortality events of the type described in Rutherford and Houde (1995). Klauda et al. (1980) noted that striped bass year-class strength, indexed by juvenile abundance, varied about 34-fold in the Hudson River, about 47-fold in Chesapeake Bay, and 160-fold in the Roanoke River (where upstream water temperatures are controlled by water regulation). The different lengths of the data sets, as well as the fact that Chesapeake Bay juvenile index reflects a mix of fish derived from tributaries and the Bay proper, make this comparison somewhat problematic to interpret. What is likely is that increased physical variability in smaller estuaries translate into greater recruitment variability.

Further, evidence from smaller streams suggests that recruitment improves in years with greater spring runoff (McGovern and Olney, 1996; Kellogg

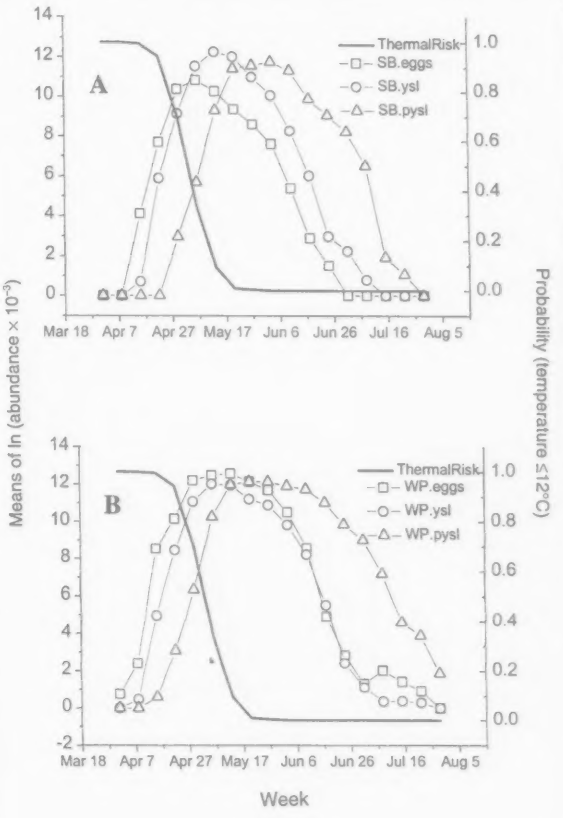

Figure 5

Probability of water temperature occurring at or below 12°C in Hudson River (based on 40-year database: Poughkeepsie Water Works, Poughkeepsie, NY) compared with means of log-transformed, river-wide abundances (1000s) of early life stages of (**A**) striped bass and (**B**) white perch. Squares = eggs, circles = yolksac larvae, and triangles = postyolksac larvae.

et al.[3]). Increased runoff in small streams could translate into more available habitat for larvae, including greater food availability (Bulak et al. 1997; Kellogg et al.[3]). Larger watercourses like the Hudson should, on average, provide a more constant amount of suitable habitat between years.

Further, we suggest that biotic controls on recruitment, if not as easily assessed as temperature and discharge, may play relatively greater roles in larger estuaries than in smaller ones, or at least in those systems with relatively predictable physical forcing. Our results implicate biotic factors for one year class of striped bass in the Hudson and are based on a comprehensive approach that included careful observation of larvae and retrospective analysis of juvenile early life histories. Had we not carried out the retrospective analysis, we likely would have predicted that later cohorts would have had the greatest recruitment potential.

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Biology of a deep benthopelagic fish, roudi escolar *Promethichthys prometheus* (Gempylidae), off the Canary Islands

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Abstract—The roudi escolar *Promethichthys prometheus* is common in deep hook-and-line and longline catches of a small-scale fishery along the slope off the Canary Islands. Population structure, reproduction, growth, and mortality of the species were studied from sampling undertaken from August 1992 to July 1995. Range of length of fish in the catches was between 36 and 80 cm TL, with a main distribution between 56 and 66 cm. The overall ratio of males to females was 1:1.74. Females predominated in all sizes. The sex ratio varied throughout the period of study; the lowest discrepancy between males and females, however, was during the reproductive period. A vertical space partitioning among sexes was observed, with males predominating from 600 to 800 m depth, females from 300 to 500 m. The reproductive period of the species was from April to September, with a peak in spawning in June–July. The size at first maturity was 47.41 cm. The parameters of the length-weight relationship for all fish were a=0.004521 and b=2.98932. Age readings of otoliths indicated that the exploited population consisted of nine age groups (III–XI years). The von Bertalanffy growth parameters for all individuals were L_∞=93.61 cm, k=0.18/years, and t_0 =–1.54 years. The rates of mortality for all fish were Z=0.49/years, M=0.35/years, and F=0.14/years. The length at first capture for the whole population was 51.57 cm.

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The family Gempylidae consists of 16 genera and 23 species. Only seven species are found off the Canary Islands, one of which is the roudi escolar *Promethichthys prometheus* (Cuvier, 1832), the only species recognized to date in the genus *Promethichthys* (Nakamura and Parin, 1993).

The roudi escolar is a benthopelagic marine fish that has a worldwide distribution in tropical and warm temperate waters. This species generally inhabits waters between 100 and 800 m in depth over seamounts and continental and insular slopes. It migrates upward at night, probably forming schools (Nakamura, 1981; Parin, 1986; Nakamura and Parin, 1993).

Published information on *P. prometheus* is very scarce. The majority of studies describe its morphological characteristics, geographical and depth distribution, and ecology (Nakamura, 1981; Parin, 1986; Nishikawa, 1987; Nakamura and Parin, 1993). Only Lorenzo and Pajuelo (1995) have studied some biological aspects of the species. These authors carried out a preliminary study on the sex ratio, reproduction, and age and growth of roudi escolar off the Canary Islands (central-east Atlantic) on the basis of a small number of specimens during one life cycle. This paper is an extension of their work, analyzing, in addition to all those aspects, population structure and mortality.

The roudi escolar is common in the catches of the deep hook-and-line and longline small-scale fishery over the slope off the Canary Islands. In this area, this species is captured year round without significant seasonal differences in landings.

Materials and methods

Between August 1992 and July 1995, the TL (cm) of 1879 specimens of roudi escolar was measured monthly from commercial catches of the small-scale fleet. Fish were caught with baited hook-and-lines and longlines at depths of 285–870 m around the islands of the Canary archipelago (Fig. 1).

A subsample was taken by a random stratified method from each sample for biological examination. In total, 776 individuals were analyzed. For each fish, the TW (0.1 g) and the weight of the gonads (0.01 g) were measured, and sex and stage of maturation were ascertained macroscopically. The latter was classified as follows: I = immature; II = resting; III = ripe; IV = ripe and running; V = spent. Sagittal otoliths of the fish were extracted, cleaned, and stored dry. The length-frequency distribution of individuals in catches was calculated. Data were pooled for 1992–95.

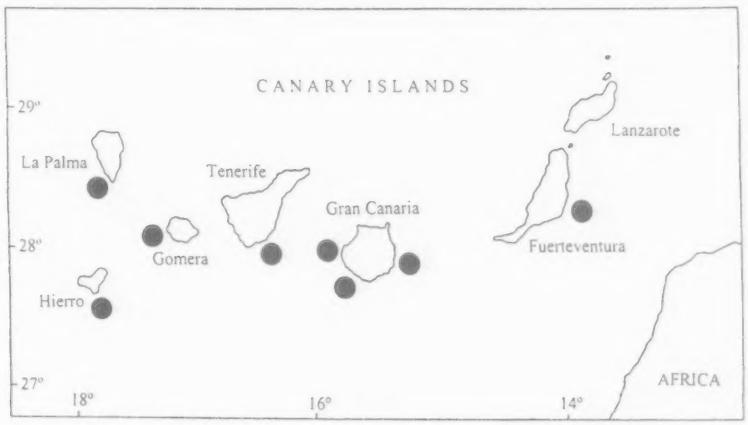

Figure 1
Location of sampling areas (●) in the Canary Islands.

The sex ratios (males:females) for the whole sample, for different size classes, for quarters of a year, and for depth strata were calculated. The reproductive season was determined on the basis of monthly variations of the gonadosomatic index (GSI) according to Anderson and Gutreuter (1983). The length at sexual maturity (length at which fifty percent of the specimens became mature) was estimated by means of a logistic function that was fitted to the proportion of the mature individuals (stages III, IV, and V) by using a nonlinear regression (Saila et al., 1988).

The ratio of total length to total weight was calculated over the whole period for males and females separately, as well as for the population as a whole, by applying a linear regression (Ricker, 1973). Age was determined by interpreting growth rings on the otoliths; whole otoliths were placed in a watch glass with a blackened bottom and containing glycerin and examined under a compound microscope with reflected light. Counts for each specimen were performed at least twice and only coincident readings were accepted. An index of average percent error (APE) developed by Beamish and Fournier (1981) was used to compare the precision of age determinations. Ageing was validated indirectly by examination of monthly changes in appearance of the margins of the otoliths (Morales-Nin, 1987). The date 1 July was considered as birthdate to assign the individual ages to age groups. The von Bertalanffy growth curve was fitted to data of the resulting age-length key by means of the Marquardt's algorithm for nonlinear least squares parameter estimation (Saila et al., 1988).

Length-frequency data were converted to age frequencies by using the estimated von Bertalanffy growth parameters (Pauly, 1983, 1984). The rate of total mortality (Z) was calculated from the length converted catch curve by using ELEFAN program (Gayanilo et al., 1988). The rate of natural mortality (M) was determined from the equation of Pauly (1980). Following estimation of Z and M, the rate of fishing mortality (F) was calculated by substraction. The length at first capture was estimated from the selection ogive generated from the length converted catch curve (Pauly, 1984).

Results

The size-frequency distribution showed a length range of 36 to 80 cm TL in the catches, with a main distribution between 56 and 66 cm (Fig. 2).

Of the 776 fish examined, 282 (36.3%) were male, 491 (63.3%) female. The sex of the remaining 3 (0.4%) individuals could not be identified macroscopically because they were immature and had very thin, translucent gonads. The overall ratio of males to females was 1:1.74 and χ^2 analysis revealed this to be significantly different from a 1:1 ratio (Table 1). Females predominated in all size intervals. Sex ratios for males and females grouped into 5-cm length classes had significant departures from the 1:1 ratio for all size intervals (Table 1). The ratio of males to females varied throughout the period of study, but there were no significant differences from the 1:1 ratio during the spring and summer months (Table 2). There was a relationship between the sex of roudi escolar and depth; males predominated at 600 to 800 m depths, females at 300 to 500 m (Table 3).

The GSI showed higher values for females than for males (Fig. 3). The same temporal variation pat-

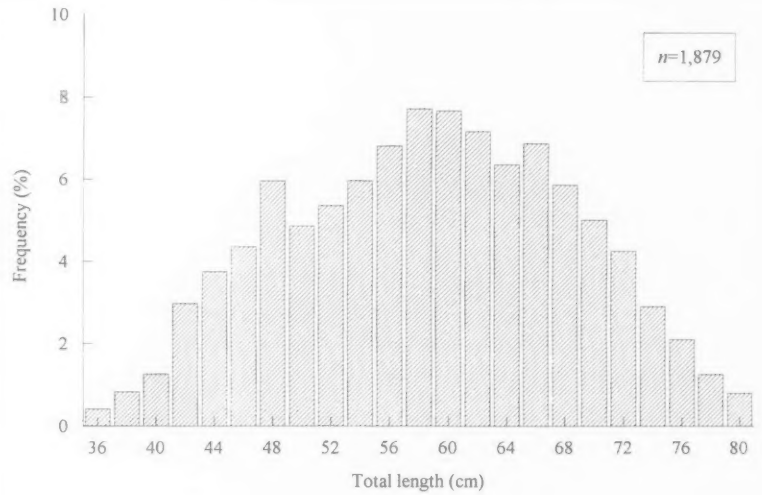

Figure 2

Length-frequency distribution for *P. prometheus* caught off the Canary Islands (August 1992–July 1995).

Table 1

Number of males and females of *P. prometheus* caught off the Canary Islands by 5-cm size class and sex ratio tested by chi-square analysis. *=$\chi^2 > \chi_t^2{}_{1,0.05}=3.84$.

Length (cm)	Males	Females	Sex ratio	χ^2
35.1–40.0	5	14	1:2.80	4.26*
40.1–45.0	21	40	1:1.90	5.91*
45.1–50.0	29	52	1:1.79	6.53*
50.1–55.0	45	71	1:1.57	5.82*
55.1–60.0	60	94	1.1.56	7.50*
60.1–65.0	48	84	1:1.75	9.80*
65.1–70.0	36	62	1:1.72	6.89*
70.1–75.0	26	48	1:1.76	6.54*
75.1–80.0	12	26	1:2.16	5.15*
Total	282	491	1:1.74	56.50*

Table 2

Number of males and females of *P. prometheus* caught off the Canary Islands by quarter and sex ratio tested by chi-square analysis. *= $\chi^2 > \chi_t^2{}_{1,0.05}=3.84$.

Quarter	Males	Females	Sex ratio	χ^2
3/92	16	23	1:1.44	1.25
4/92	13	35	1:2.69	10.08*
1/93	13	37	1:2.85	11.52*
2/93	24	37	1:1.54	2.77
3/93	24	34	1:1.42	1.72
4/93	14	38	1:2.71	11.07*
1/94	29	51	1:1.75	6.05*
2/94	36	49	1:1.36	1.98
3/94	39	50	1:1.28	1.35
4/94	24	44	1:1.83	5.88*
1/95	31	59	1:1.90	8.71*
2/95	19	34	1:1.79	4.24*

tern was recorded for both sexes. Highest values occurred between April and September, peaking during June–July. From October to March the values were low.

No significant difference in length at sexual maturity was found between males and females (t-test, $t=1.31<t_{0.05,385}=1.65$). The length at which fifty percent of the fish became mature was 47.41 cm TL (Fig. 4).

Males were found to be between 38 and 80 cm TL, females between 36 and 80 cm. The length range of immature individuals was from 36 to 38 cm. The parameters of the total length to total weight relationship for males and females separately, and for the population as a whole, are given in Table 4. No significant difference in the allometric coefficient was found between males and females (t-test, $t=1.53<t_{0.05,771}=1.65$). Isometric growth was observed in both sexes and for the whole population (Table 4).

Of the otoliths examined, 670 (86.4%) were readable and used for the study of age and growth. The

APE value was only 3.4%. A false hyaline ring interrupting the normal growth pattern of the otolith was identified within the fourth annual opaque zone and in all subsequent opaque zones. Marginal zone analysis showed that one annulus was formed per year (Fig. 5). The percentage of otoliths with opaque edge was high in the months from April to September, and between June and August in particular.

Fish aged 3 to 11 years were present in the samples (Table 5). Growth parameters determined for males, females, and the entire population are shown in Table 6. No significant differences in the growth parameters were found between sexes (Hotelling's T^2-test, $T^2=5.29<T_{0\ 0.05,3,666}^{2}=7.88$).

The length converted catch curve is shown in Figure 6. The rates of total mortality, natural mortality, and fishing mortality were $Z=0.49$/year, $M=0.35$/year, and $F=0.14$/ year, respectively. The size at first capture was 51.57 cm TL.

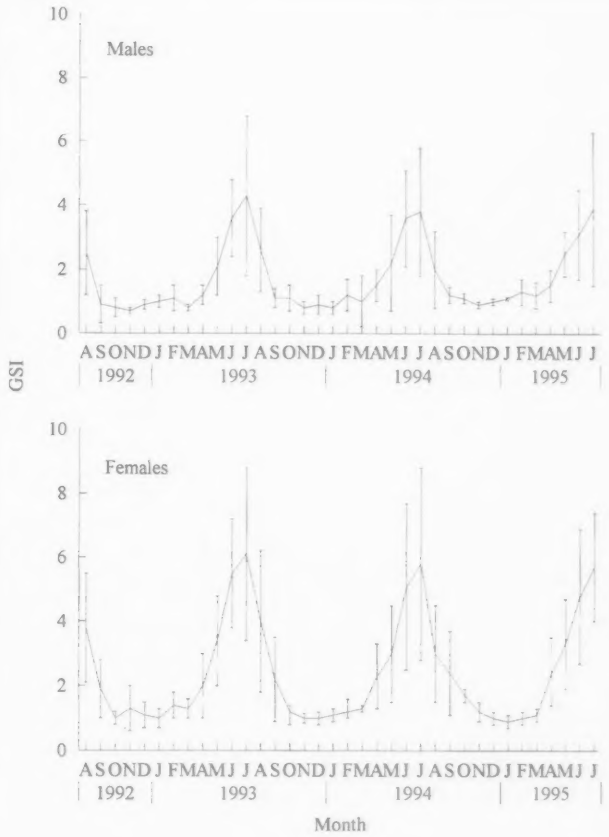

Figure 3

Monthly evolution of the gonadosomatic index (GSI) for males and females of *P. prometheus* caught off the Canary Islands (August 1992–July 1995).

Discussion

Promethichthys prometheus is distributed along the slope to a depth of 800 m (Nakamura and Parin, 1993). In waters off the Canary Islands, greatest concentrations of this species are found between 400 and 700 m depth. Below this depth, the species is replaced by other trichiuroid fish present in the area, e.g. the black scabbardfish, *Aphanopus carbo* Lowe, 1839 (Uiblein et al., 1996).

The roudi escolar off the Canary archipelago is a gonochoristic species with no evidence of sexual dimorphism. The sex ratio is clearly unbalanced in favor of females. This fact could be explained by the differences between sexes in the spatial distribution. The lowest discrepancy between sexes observed during the reproductive season seems to confirm this conclusion. Because of the space partitioning between sexes and because females are fished more than males, this species could be classed as vulnerable to unrestrained fishing. Therefore, fishing for roudi escolar is an activity that has the potential to threaten its target population compared with fishing for more reliable and robust stocks (Csirke, 1988). This fishery will require a prudent exploitation strategy to reduce the potential risk of a collapse.

The roudi escolar has a definite reproductive period (extending from April to September, with a peak in spawning activity in June–July) which agrees with information reported by Parin (1986) and Nakamura and Parin (1993). These authors pointed out that the

Table 3

Number of males and females of *P. prometheus* caught off the Canary Islands by depth stratum and sex ratio tested by chi-square analysis. $*=\chi^2>\chi_{t\ 1.0.05}^{2}=3.84$.

Depth (m)	Males	Females	Sex ratio	χ^2
201–300	4	26	1:6.50	16.13*
301–400	21	136	1:6.47	84.23*
401–500	35	187	1:5.34	104.07*
501–600	28	39	1:1.39	1.81
601–700	76	48	1.0.63	6.32*
701–800	85	41	1:0.48	17.12*
801–900	32	12	1.0.37	9.09*

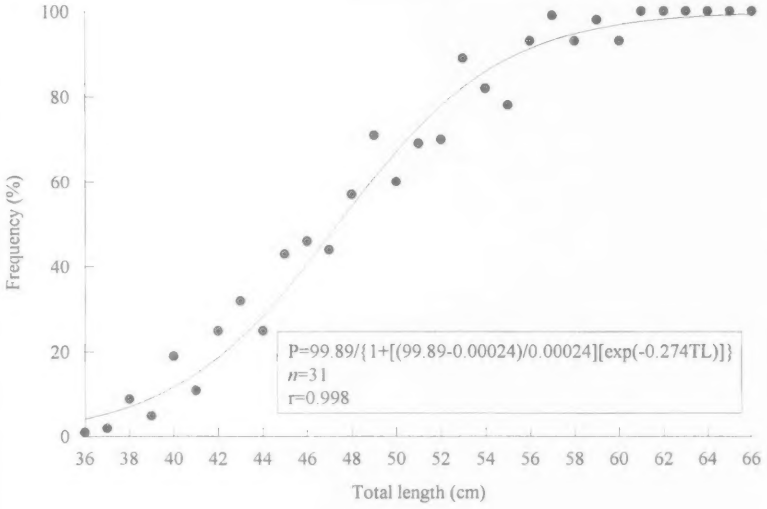

Figure 4

Sexual maturity ogive for *P. prometheus* caught off the Canary Islands (August 1992–July 1995).

spawning of this species occurs from August to September in the Atlantic off Madeira. Nishikawa (1987) found the highest concentration of gempylid larvae at the end of the summer months in the Pacific waters of Japan. In the Canary archipelago, the spawning of roudi escolar seems to be related to water temperatures, occurring when these reach greatest values. Possible significance of seasonal temperature variation to maturation and spawning in other bony fish species off the Canary Islands has been discussed by Lorenzo and Pajuelo (1996) and Pajuelo and Lorenzo (1995, 1996). Reproduction in roudi escolar does not involve horizontal migrations because during the spawning season the specimens are observed in the same areas where they are fished all year round. The lowest discrepancy in the number of males and females observed during the spawning period suggests an aggregation for breeding. Males and females were found aggregated mainly at depths of 450–650 m during this period.

Length at sexual maturity does not differ between males and females, corresponds approximately to 48 cm TL. In the age-length relationship, this size corresponds to 4-year-old specimens. The size at which fifty percent of the fish become mature is less than the length at first capture and the majority of the total catch is longer than this length, indicating a good exploitation pattern from the biological point of view. Furthermore, a low value of fishing mortality rate was obtained.

Table 4

Parameters of the length-weight relationship for males, females and all fish of *P. prometheus* caught off the Canary Islands and the possibility of isometry tested by Student's *t*-test. *= $t > t_{0.05,n>250} = 1.65$.

	a	b	SE(b)	r^2	n	t-test
Males	0.004128	2.95321	0.03721	0.959	282	1.25
Females	0.004987	2.96214	0.03140	0.981	491	1.20
All fish	0.004521	2.98932	0.02341	0.992	776	0.45

The alternate pattern of opaque with translucent zones was easily distinguishable on the otoliths of the roudi escolar. These zones are deposited owing to alternating periods of rapid and slow growth (Williams and Bedford, 1974). The opaque zone is formed when the water temperature is higher, and food is abundant, and the translucent is formed when temperature is lower and the species spawns. This finding demonstrated the validity of using otoliths for estimating the age and growth of roudi escolar. The false hyaline zones observed within the fourth opaque ring and in subsequent opaque rings are probably spawning bands, because this species spawns in the summer months, when the opaque zone is formed in the otoliths. Morales-Nin (1987) pointed out that when the spawning does not take place during the period of hyaline zone formation, a false ring, known

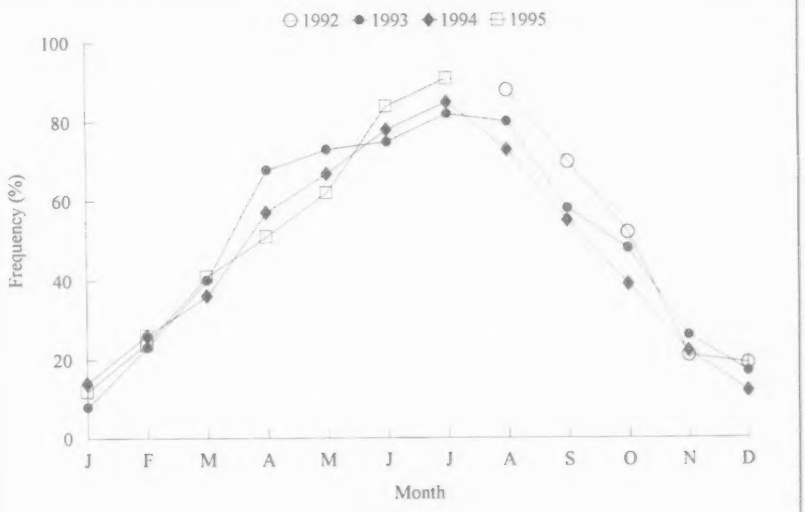

Figure 5

Monthly percentage of otoliths with opaque edge for *P. prometheus* caught off the Canary Islands (August 1992–July 1995).

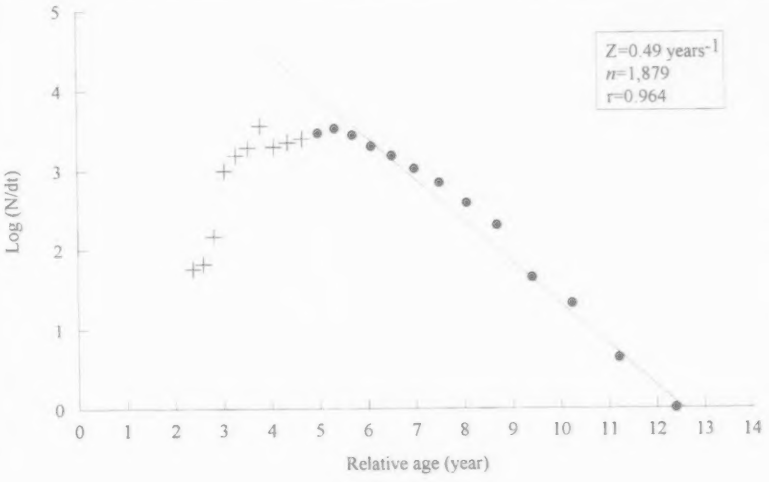

Figure 6

Length converted catch curve for *P. prometheus* caught off the Canary Islands (August 1992–July 1995). The initial data points (+) were not used in the regression.

as a spawning ring, may form within an opaque zone, dividing it into two.

The oldest age class observed was XI years, although this class, as well as age classes IX and X, were poorly represented in the landings. As a whole, growth of the roudi escolar is relatively fast and males and females grow at equal rates. The growth parameters obtained are reasonable because the theoretical maximal length value is greater than the size of the largest fish sampled and because the growth coefficient value indicates relatively rapid attainment of maximal size.

Table 5

Age-length key for all fish of *P. prometheus* caught off the Canary Islands.

Size (cm)	Age group (years)								
	III	IV	V	VI	VII	VIII	IX	X	XI
36	2								
37	1								
38	2								
39	4								
40	6								
41	9								
42	9	1							
43	7	3							
44	4	4							
45	3	8							
46	3	7							
47		9							
48	2	13	1						
49		17	2						
50		14							
51		7	4						
52		5	6						
53		4	8						
54		3	10	1					
55			16	3					
56		2	22	3					
57		1	19	6					
58			12	7					
59			8	11	2				
60			4	17	2				
61			2	28	3				
62			3	21	6				
63			1	11	8				
64				8	14	2			
65				7	20	1			
66				3	23	4			
67				1	16	7			
68				2	10	10	1		
69					6	12	4		
70					3	17	4		
71					2	11	7	1	
72					1	6	9	2	
73						5	9	2	
74						1	7	3	1
75						2	5	6	1
76							2	4	2
77							1	3	2
78									1
79								1	
80									1
n	52	98	118	129	116	78	49	22	8
$\bar{x}$	41.6	48.9	55.7	61.1	65.5	69.4	72.4	74.9	76.7
SD	2.4	2.8	2.6	2.6	2.4	2.2	2.0	1.8	1.7

Table 6

Parameters of the von Bertalanffy growth curve for males, females, and all fish of *P. prometheus* caught off the Canary Islands.

	L_∞ (cm)	k (per year)	t_0 (years)	r^2
Males	91.93	0.18	−1.66	0.964
Females	94.03	0.17	−1.58	0.978
All fish	93.61	0.18	−1.54	0.988

Acknowledgments

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Abstract.—We collected data on age-length and length-weight relationships, age and length at first maturity, and spawning seasons of grass rockfish, *Sebastes rastrelliger*, and brown rockfish, *S. auriculatus*, off southern California. In addition, we also collected data on fecundity of grass rockfish. For both species, males and females grew at the same rates and von Bertalanffy age-length parameters for grass rockfish were l_∞ = 51.3 cm, k = 0.11, t_0 = −2.41 and for brown rockfish l_∞ = 51.4 cm, k = 0.16, t_0 = −0.55. Male and female grass rockfish matured at about the same length and age, between 22 and 28 cm and between 2 and 5 yr. There was also little difference between the sexes for brown rockfish; they matured between 19 and 32 cm and between 3 and 6 yr. Grass rockfish spawned from January to March, peaking during January; brown rockfish spawned from January to June (and perhaps August), also peaking in January. Fecundity of grass rockfish ranged from about 80,000–760,000 eggs.

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Aspects of the life histories of grass rockfish, *Sebastes rastrelliger*, and brown rockfish, *S. auriculatus*, from southern California

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Rockfishes (Scorpaenidae: *Sebastes*) are of major commercial importance in California waters. Until recently, almost all of these fishes were landed dead, destined either to be sold whole or as fillets, as fresh or frozen products (Lea, 1992). The sale of live rockfish formed only a very small part of the commercial fishery, and most of this catch was sold in Asian markets and restaurants, particularly in San Francisco and Los Angeles. Recently, however, landings in the live fish fishery have increased sharply. Documented landings (almost certainly an underestimate of the true catch) escalated from about 52,000 pounds in 1989 to 987,000 pounds in 1995 (McKee-Lewis[1]). Live finfish caught in California waters are now widely sold in many local and overseas venues. Within the state, most of the fish destined for the live fish market are caught off southern and central California.

The live-fish fishery targets primarily those inshore species easily held alive, i.e. various rockfishes, California sheephead (*Semicossyphus pulcher*), California halibut (*Paralichthys californicus*) and cabezon (*Scorpaenichthys marmoratus*). Among the important rockfishes are grass rockfish (*S. rastrelliger*) and brown rockfish (*S. auriculatus*). Over 100,000 pounds of grass rockfish were landed in the live fish fishery in 1995 (McKee-Lewis[1]). Despite their importance to this fishery, relatively little was known of their biology.

Before our study, virtually nothing had been published on the life history of grass rockfish. They are solitary crevice-dwellers, inhabiting high relief substratum from Yaquina Bay, Oregon, to Bahia Playa Maria, central Baja California (Miller and Lea, 1972). Grass rockfish are among the shallowest-dwelling rockfishes, found from the intertidal waters to 46 m, usually to depths of about 10 m (Feder et al., 1974; Eschmeyer et al., 1983; Yoshiyama et al., 1986). Grass rockfish feed on fishes, crabs, shrimps, and other crustaceans (Quast, 1968; Grossman, 1986).

Somewhat more was known regarding brown rockfish, which range from Prince William Sound, northern Gulf of Alaska, to Bahia San Hipolito, central Baja California, and which inhabit subtidal waters to depths of 135 m (Love et al.[2]). Unlike grass rockfish, brown

[1] McKee-Lewis, K. 1994. California Department of Fish and Game, Marine Resources Division, 4949 Viewridge Ave., San Diego, CA. Personal commun.

[2] Love, M. S., L. Thorsteinson, C. W. Mecklenburg and T. A. Mecklenburg. 1998. A checklist of marine and estuarine fishes of the Northeast Pacific, from Alaska to Baja California. Biological Resources Division, U. S. Geological Survey.

rockfish may be found in small aggregations. The young are often found in nearshore bays, often around piers or over rubble. Older fish tend to move out of shallow waters and live over both high and low relief, often near the sand-rock interface (Matthews, 1990; Adams, 1992). Brown rockfish feed on crustaceans and fishes (Quast, 1968; Washington et al.[3]). In Puget Sound, spawning occurs during June, whereas off central California larvae are released in December–January and May–June (Wyllie Echeverria, 1987; Washington et al.[3]). There has been no published information on growth rates. In addition, despite their importance, little work on this species has been conducted in southern California.

Knowledge of the life history of a species is an essential prerequisite for effective fisheries management. Our goal was to fill gaps in knowledge of the basic life history of these two species in southern California waters.

Methods

We collected 162 grass rockfish during 1984 and 1996 and 367 brown rockfish between 1977 and 1995. All were collected from southern California waters by spear or hook and line. Data collected included total length (cm), weight (g), sex, capture location, and collection date. In the laboratory, we weighed the gonads, assessed reproductive state, and removed sagittal otoliths.

Age determination

Otoliths were placed on wood blocks and embedded in clear epoxy. Each block with its otoliths was placed on a Buehler Isomet low-speed saw, and an 0.05-cm wafer (transverse section) was cut from it with two diamond-edge blades separated by a stainless steel shim. Before reading, the wafers were burned slightly over an alcohol lamp. The wafers were then placed in a water-filled, black-bottomed watch glass and examined under a dissecting microscope.

Ages were assigned by direct observation of otolith annuli. We aged a total of 149 grass rockfish, including 78 males (16.6–47.5 cm) and 71 females (14.4–50.5 cm), as well as 269 brown rockfish, including 120 males ranging in length from 15.0 to 49.8 cm and 149 females ranging from 17.2 to 53.2 cm. Growth was assumed to be described by the von Bertalanffy growth curve model (von Bertalanffy, 1938):

$$l_t = l_\infty\left(1-e^{-k(t-t_0)}\right),$$

where l_t = length at time t;
l_∞ = theoretical maximum length;
k = constant expressing the rate of approach to l_∞; and
t_0 = theoretical age at which $l_t = 0$.

Growth equation constants for the von Bertalanffy growth model were calculated from length-at-age data for each species by using the least-squares, nonlinear regression (SYSTAT, 1992).

Maturation and reproduction

We estimated length and age at first maturity by classifying gonads as immature or mature on the basis of criteria given in Westrheim (1975), Gunderson (1977), and Love and Westphal (1981). As with other rockfishes, it was difficult to distinguish between immature and mature resting-stage females during the nonreproductive season. Thus, we did not use females captured during the nonreproductive season for either the length-maturity or age-maturity analyses.

The relationships between length and maturity and age and maturity were established by using a natural log transformation of the equation

$$P_x = \frac{1}{1+e^{ax+b}}$$

(Gunderson et al., 1980) to yield

$$\ln\frac{(1-P_x)}{P_x} = ax+b,$$

where p_x = the proportion mature at length or age x; and
a and b = fitted parameters.

We then plotted x against

$$\ln\frac{1-P_x}{P_x}$$

using simple linear regression to estimate values for a and b. Fifty-percent maturity was calculated by using fitted values of a and b, and by using $p_x = 0.50$ to solve for x.

A gonadosomatic index [(gonad weight)/(total body weight) × 100] was computed to quantify changes in gonad size with season. Gonad condition (immature, resting, vitellogenesis, eyed, spawned [Wyllie Echeverria, 1987]) was determined for each female.

We determined egg production in grass rockfish, counting subsamples of unfertilized eggs. Eggs were

[3] Washington, P. M., R. Gowan, and D. H. Ito. 1978. A biological report on eight species of rockfish *Sebastes* spp. from Puget Sound, Washington. Northeast Alaska Fisheries Center, Processed Rep., 50 p.

excised from the ovarian membrane and placed in Gilson's solution (equal parts concentrated glacial acetic acid, chloroform, and 60% ethanol) for about three months and shaken periodically to loosen them from ovarian tissue. Before counting, the ovaries were repeatedly washed and the egg masses broken up to remove remaining connective tissue. The resulting eggs were weighed; the subsamples were removed and also weighed. Eggs in each subsample were counted and the mean number per weight calculated for each subsample. Egg production, F, was estimated by the calculation

$$(TW \times SN) / (SW),$$

where TW = total weight of gonads;
SN = mean subsample egg number; and
SW = subsample weight.

Results

Age and growth

For each species, the von Bertalanffy parameters were estimated for males and females separately, and for both sexes combined. An ANOVA was used to statistically compare the amount of variance described by both the separate and combined growth curves. ANOVA results concluded that for both grass rockfish (F=1.16, P>0.05) and brown rockfish (F=1.15, P>0.05) there was no significant difference in the amount of variance explained by estimating sex-specific values for the three parameters. Thus, for each species growth of both sexes is adequately depicted by a single growth curve.

The von Bertalanffy parameters for grass rockfish were L_∞ = 51.3 cm, k= 0.11, t_0 = –2.41 (Fig. 1) and for brown rockfish L_∞ = 51.4 cm, k = 0.16, t_0 = –0.55 (Fig. 1). As with other rockfishes, immature fishes grew relatively rapidly slowly as they matured. Within each species, sexes appeared to have similar life spans. The oldest male grass rockfish was 22 yr, the oldest female 23 yr. Male brown rockfish lived to 18 yr, females to 20 yr.

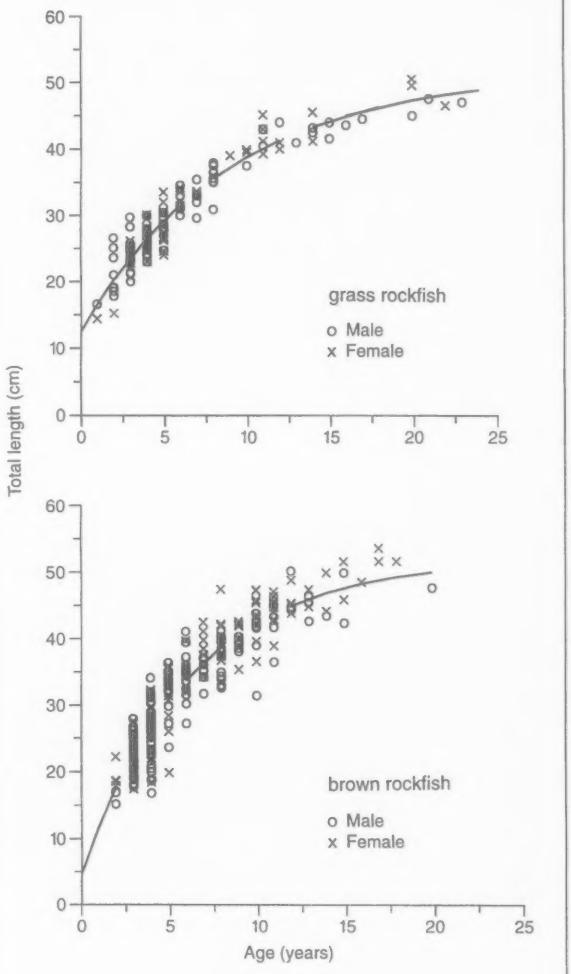

Figure 1
Von Bertalanffy growth curves for grass rockfish (*S. rastrelliger*) and brown rockfish (*Sebastes auriculatus*) from southern California.

Length-weight relationships

For both species, the relationship between total length and weight fitted the relationship

$$W = aL^b,$$

where W = weight in grams;
L = total length in centimeters; and
a and b = constants.

Parameters were estimated with Fishparm v. 3.0 (Saila et al. 1988) by using Marquardt's algorithm for nonlinear least squares parameter estimation.

To test for differences in the relationships between sexes, male and female data within a species were modeled separately. Each relationship was then $\log_{10}$-transformed to create a linear equation, and slopes of the male and female models were compared by using Student's t-test. This process was repeated with gonad weight subtracted from total body weight, to

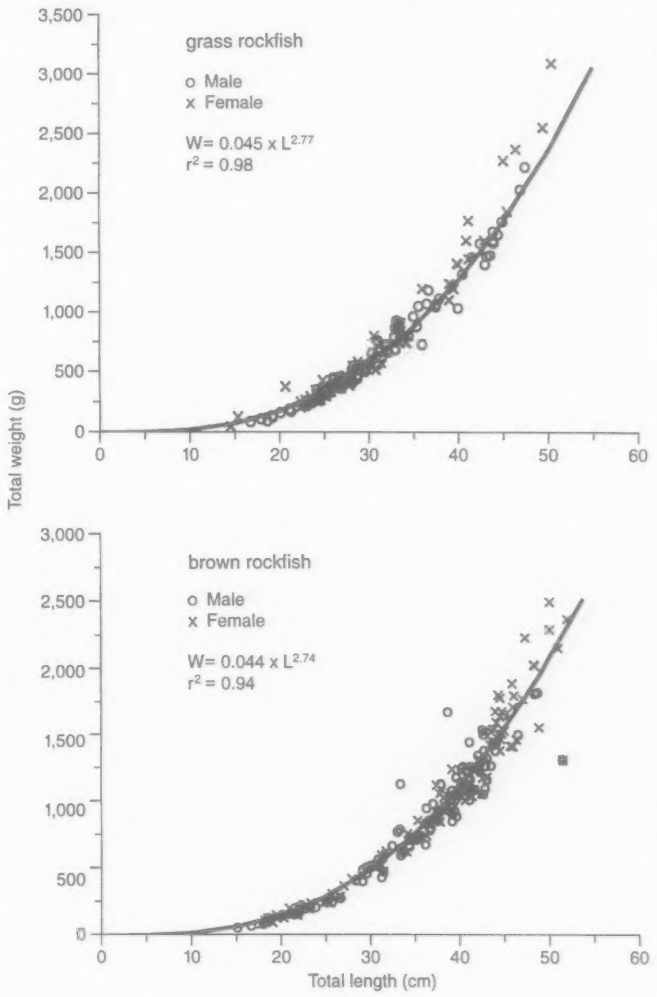

Figure 2

Length-weight relationships for grass rockfish (*S. rastrelliger*) and brown rockfish (*Sebastes auriculatus*) from southern California.

determine if any difference was simply an artifact caused by the larger female gonads.

For grass rockfish, 86 males and 73 females were measured and weighed. Although female grass rockfish tended to be heavier than males at a given length (T-test, t=2.21, P<0.05), the difference was not evident when gonad weight was subtracted from total body weight (T-test, t=1.66, P>0.05), and we therefore have combined these data into a single figure (Fig. 2).

A total of 116 male and 102 female brown rockfish were sampled. For brown rockfish, there was no significant difference in weight at a given length between males and females (T-test, t=0, P>0.05); we have also combined these data into a single figure (Fig. 2).

Length and age at first maturity

For these analyses, we examined 53 female and 64 male grass rockfish and 135 female and 129 male brown rockfish. Both male and female grass rockfish matured over relatively narrow length and age intervals (Table 1; Fig. 3). Both sexes began to mature at 22 cm and all fish were mature by 28 cm.

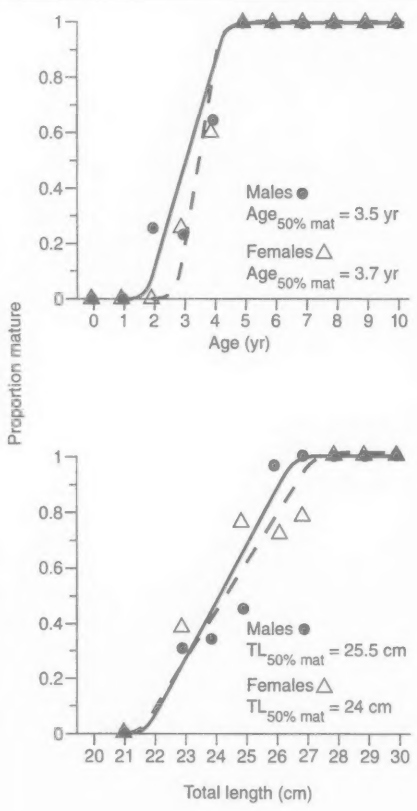

Figure 3

Age-maturity and length-maturity and relationships for male (n=88) and female (n=74) grass rockfish (*Sebastes rastrelliger*) taken in the southern California Bight, including estimated ages and lengths at which 50% of the fish were mature. Solid and dashed lines represent predicted relationship.

Table 1

Maximum-likelihood estimates for the parameters of the logistic equation relating proportion mature to lengths and ages of grass and brown rockfishes. Predictive length ($l_{0.50}$) and age ($Age_{0.50}$) at 50% maturity and mean square error (MSE) of the logistic equation are also presented.

	Length			
Species	a	b	$l_{0.50}$ (cm)	r^2
Grass rockfish				
Male	0.83	20.62	24.5	0.97
Female	0.73	17.49	24.0	0.97
Brown rockfish				
Male	0.38	9.47	25.0	0.85
Female	0.62	16.36	26.4	0.99
	Age			
Species	a	b	$Age_{0.50}$	r^2
Grass rockfish				
Male	1.52	5.36	3.5	0.93
Female	1.95	7.20	3.7	0.99
Brown rockfish				
Male	1.57	6.05	3.9	0.99
Female	1.79	7.51	4.2	0.99

Fifty percent of males were mature at about 24.5 cm, and fifty percent of females at 24 cm. Male grass rockfish matured from 2 to 5 yr, females from 3 to 5 yr.

For brown rockfish, there was also little difference between sexes in either length or age at first maturity (Table 1). Males matured between 19 and 29 cm, females between 21 and 32 cm (Fig. 4). For males, 50% maturity occurred at about 25 cm, for females at 26.4 cm. Age at first maturity for both male and female brown rockfish occurred as early as 3 yr, and all fish were mature by 6 yr (Fig. 4).

Spawning seasons

Grass rockfish released larvae from January to March, reaching a peak in spawning during January (Fig. 5). Females with spawned ovaries were found only during February and March, after which followed a 6-month resting stage. Vitellogenic ovaries were common from December to February. Ovary indices remained at a minimum throughout spring, summer, and early fall, averaging about 0.3% of body weight, then increased to a peak of 6.8% in December (Fig. 6). Testes indices were also low during spring and summer (averaging less than 0.1%), rising to a peak of 0.2% in December (Fig. 6).

Brown rockfish spawned from January to August, reaching a peak in January (Fig. 5). Although females with resting stage ovaries were found from April to November, most occurred during the summer. We found vitellogenesis-stage ovaries during most months, particularly between fall and spring. For females, gonosomatic indices were lowest (averaging 0.6%) from June to November and peaked during January at 7.1% (Fig. 6). Testicular indices were lowest from March to August (averaging 0.15%) and peaked in October at 0.62% (Fig. 6).

Fecundity

The relation between grass rockfish fecundity and total length (Fig. 7) was best described by the function

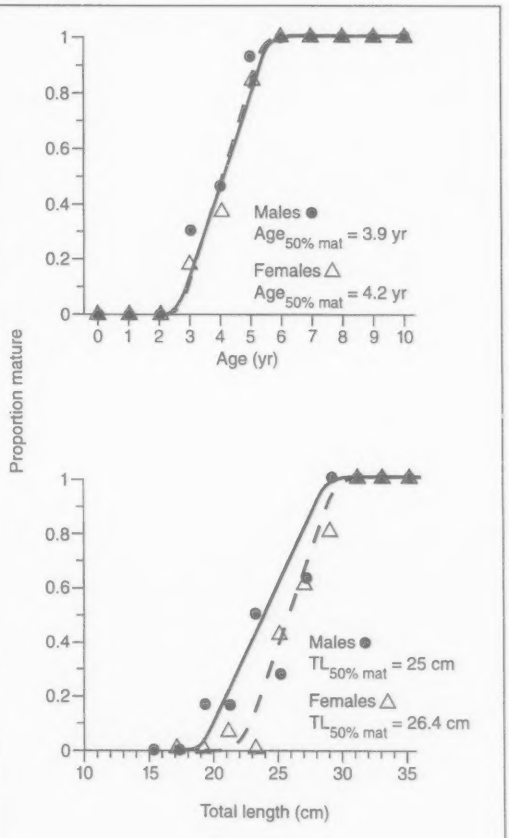

Figure 4

Age-maturity and length-maturity relationships for male (n=120) and female (n=149) brown rockfish (*Sebastes auriculatus*) taken in the southern California Bight, including estimated ages and lengths at which 50% of the fish were mature. Solid and dashed lines represent predicted relationship.

$$F = aL^b,$$

where F = number of eggs in thousands;
L = total length in centimeters; and
a and b = constants.

The value of the parameters a and b were estimated by fitting the linear function $\log F = \log a + b \log L$ by least squares. Estimated fecundity ranged from 80,000 eggs for a 26 cm TL individual to about 760,000 for one 46.5 cm long.

Discussion

In the northeast Pacific, rockfish growth rates, as measured by the term k, are quite variable (Love et al., 1990), although compared to many other groups, their growth rates are quite low (Beverton and Holt, 1960). The largest species of rockfishes tend to grow slowest (k=0.05, rougheye rockfish, *S. aleutianus*) and dwarf species exhibit relatively rapid growth (k=0.45, halfbanded rockfish, *S. semicinctus*). However, between these extremes there is no relation between maximum size and growth rate. Grass rockfish and brown rockfish growth rates are near the mean for the genus (Love et al., 1990). However, what was usual for the rockfishes was a lack of sexual dimorphism in growth rates. In most species, females grow faster than males, particularly after maturity.

Compared with most other eastern Pacific rockfishes, both species are short-lived. Of the 38 species for which we judge that fairly accurate maximum ages are known, only eight had life spans that were similar to or less than grass and brown rockfishes (Love et al.[4]). Most species lived to more than 30 years, a majority to more than 40 years. Short-lived species tend to be dwarf taxa, such as shortbelly (*S. jordani*), Puget Sound (*S. emphaeus*), squarespot (*S. hopkinsi*), and honeycomb (*S. umbrosus*) rockfishes.

For brown rockfish, there appears to be little difference in age and length at 50% maturity throughout much its range (Table 2). Although fish off central and northern California are older and larger at 50% maturity, those from Washington State and southern California are almost identical. Latitudinal differences in length or age of maturation, or both, occur in a number of rockfish species (e. g. splitnose rockfish, *S. diploproa*; widow rockfish, *S. entomelas*; yellowtail rockfish, *S. flavidus*; black rockfish, *S. melanops*; bocaccio, *S. paucispinis*) with fishes from higher latitudes generally maturing when larger or older or both (Wyllie Echeverria, 1987; Love et al., 1990; Field, 1984). However, this difference does not occur in greenstriped rockfish, *S. elongatus* (Love et al., 1990). Although it is likely that environmental parameters (e.g. water temperature, food availability, growth seasons) play a role in this phenomenon, it is not yet clear how they interact.

With 50% mature at age 4, both grass rockfish and brown rockfish mature at a young age compared with many rockfishes. Off California, most species reach 50% maturity at between 4 and 8 years (Wyllie Echeverria, 1987; Love et al., 1990); thus these two species fall in the younger part of that range. Dwarf species, such as shortbelly rockfish (*S. jordani*), Puget Sound rockfish (*S. emphaeus*) and stripetail rockfish (*S. saxicola*) mature earliest, often when 2 or 3 years old (Moulton, 1975; Wyllie Echeverria, 1987; Love et al., 1990). At the other extreme, the largest and more northerly species, such

[4] Love, M. S., M. Yoklavich, L. Thorsteinson, J. Butler. 1998. A guide to the rockfishes of the northeast Pacific. In prep.

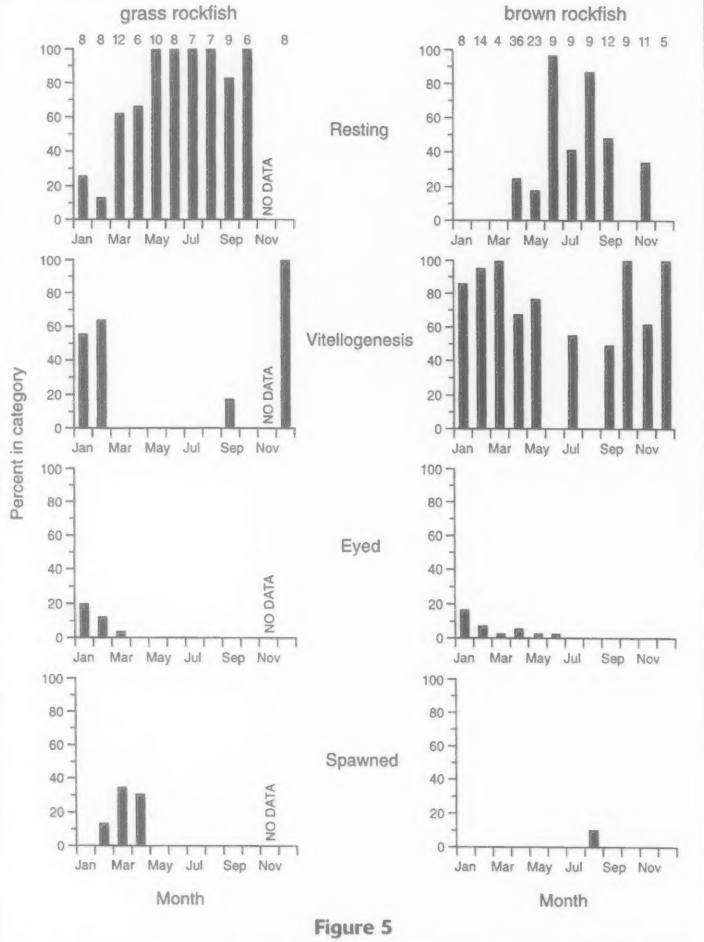

Figure 5

Percent composition by month of four gonad condition stages for female grass rockfish (*Sebastes rastrelliger*) and brown rockfish (*Sebastes auriculatus*) taken in the southern California Bight. The total number of females examined per month is listed at the top of each month in the "resting" section.

Table 2

Age and length at 50% maturity for male and female brown rockfish by area. Data from Washington State from Washington et al. (1978) and from northern-central California from Wyllie Echeverria (1987). Lengths of Washington fish are converted from fork length to total length based on Echeverria and Lenarz (1984).

Sex	Washington	Northern-central CA	Southern CA
Male	4 yr, 24 cm	5 yr, 31 cm	4 yr, 25 cm
Female	4 yr, 26 cm	5 yr, 31 cm	4 yr, 27 cm

as yelloweye rockfish (*S. ruberrimus*) and rougheye rockfish (*S. aleutianus*) may take 20 years or more to mature (McDermott, 1994; O'Connell[5]).

[5] O'Connell, T. 1994. Alaska Department of Fish and Game, 304 Lake St., Room 103, Sitka, AK 99835. Personal commun.

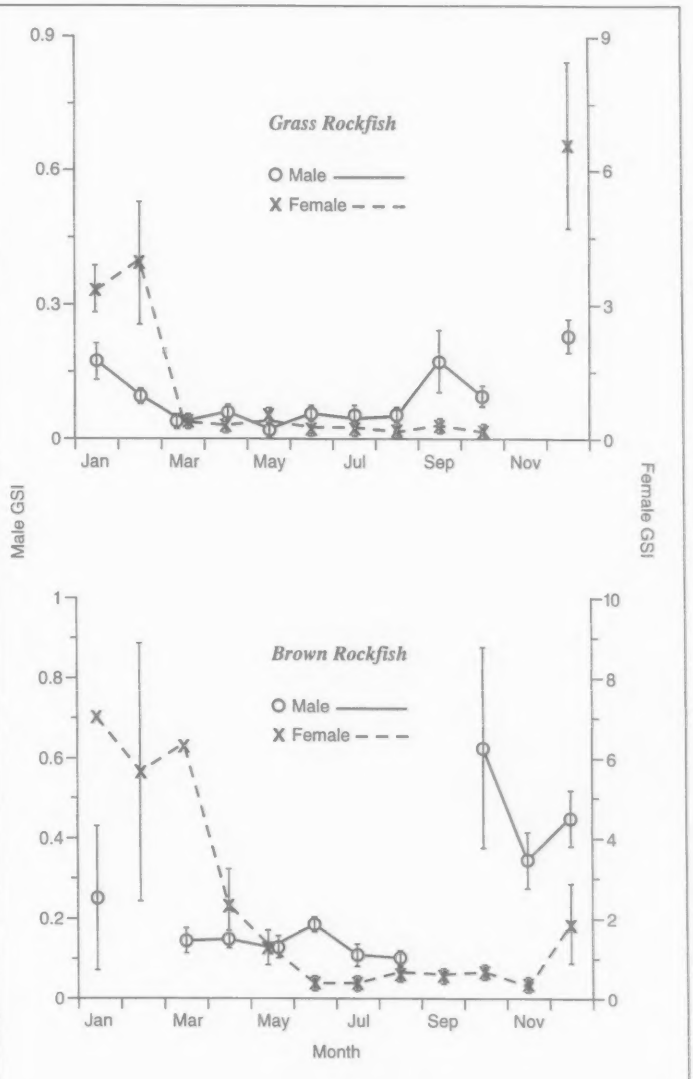

Figure 6

Seasonal changes in the gonosomatic index (GSI-gonad weight as a percent of total body weight) of male and female grass rockfish (*Sebastes rastrelliger*) and brown rockfish (*Sebastes auriculatus*). No samples of grass rockfish were taken during November and no samples of male brown rockfish were taken in February and September. Vertical lines indicate 95% confidence intervals of the mean.

Along the northeast Pacific, the vast majority of rockfish spawn in the late winter and early spring and, as with length and age at maturation, many rockfish species exhibit a latitudinal trend in spawning season. Parturition often starts earlier or is more prolonged (or both) in the southern part of a species' geographic range (O'Connell, 1987; Wyllie Echeverria, 1987; Barss, 1989; Love et al., 1990). The spawning season for brown rockfish from Puget Sound to southern California appears to follow this pattern. Spawning occurs in Puget Sound in June (Washington et al.[3]), in December–January and May–June in northern-central California (Wyllie Echeverria, 1987) and in January–August in southern California.

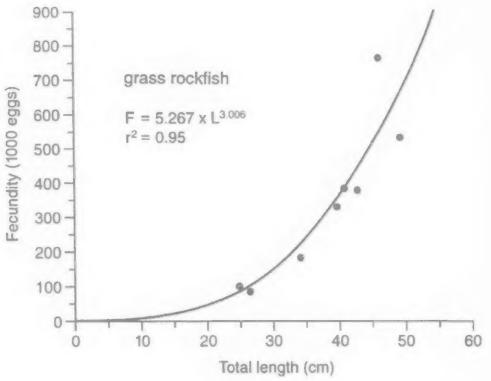

Figure 7

Fecundity-total length relationship for eight grass rockfish (*Sebastes rastrelliger*) taken in the southern California Bight.

Acknowledgments

We thank J. Harding, W. Golden, A. Amman, and L. McDonald for help in collecting some of the specimens and A. Brooks for providing analytical assistance. As always, L. Thorsteinson was very supportive of our work.

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Abstract.—Three new species of hagfish (Myxinidae, *Eptatretus*) are described from the Galápagos Islands, Ecuador. These are the first myxinids known from this region and the first species of *Eptatretus* with five, six, and eight gill pouches reported from the eastern Pacific. A key to their identification is presented.

Three new species of hagfish (Myxinidae, *Eptatretus)* from the Galápagos Islands

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The Galápagos Islands consist of about ten principal islands and over 100 smaller ones on the equator about 500 miles off the coast of Ecuador. The biodiversity found in these islands by Darwin (1896) is also expressed in the marine fauna (McCosker, 1997); three new species of hagfish were found in only eight specimens from four trap sets (Fig. 1). An exploration off South America and the Galápagos Islands in 1891 by the U.S. Fish Commission Steamer *Albatross* reported only one species of hagfish, *Myxine circifrons* Garman (1899), taken off the Gulf of Panama. Several species of *Eptatretus* with from nine to fourteen gill pouches have since been reported from the eastern Pacific coast (Wisner and McMillan, 1990), and one species with seven gills, *E. laurahubbsae* McMillan and Wisner (1984), from the Juan Fernandez Islands, Chile. The new species described below are the first hagfish reported from the Galápagos Islands, and the first *Eptatretus* with five, six, and eight gill pouches known from the eastern Pacific. Until the formation of the Panamanian land bridge there was a long-standing connection between the Caribbean and eastern Pacific, which provided a passage for hagfish to move into the eastern Pacific from the Caribbean. These new species may be more closely related to the *Eptatretus* with five to eight gills found in the Caribbean and western Atlantic than to any currently known from the eastern Pacific. Future collecting efforts along the coast of Ecuador may reveal *Eptatretus* similar to those found off the Galápagos Islands; however, until further material is available and genetic studies are made for comparison, we can only speculate on possible origins of these Galápagos hagfishes.

Although the body color of most species of *Eptatretus* is brown to black, Fernholm (1991) described a species of *Eptatretus* on the basis of one specimen with a highly unusual pink body, stating that its color was probably caused by diet. Of the eight specimens reported here, the seven larger ones are dark purplish-brown to black or dark gray where the slime has not been removed. The smallest specimen (about 142 mm), possibly an albino, is ivory to light tan. Not enough is known about the early development of hagfish to determine if this tiny specimen would have become darker with age. Albinism has been reported by Dean (1903) and Jensen (1959), and I have collected one, an adult *E. deani* (Evermann and Goldsborough, 1907), which was pinkish-white when alive and light tan color in formalin.

Head grooves are present near the eyespots of the seven large specimens, but not on the smallest hagfish. These grooves, found in many other species of *Eptatretus* (McMillan and Wisner, 1984) and once thought similar to lateral lines,

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Fish. Bull. 97:110–117 (1999).

are now believed to have no sensory purpose. Because they are not considered a species-specific character and have no taxonomic value for the present study, they are not included in the species descriptions.

Counts of cusps and total slime pores are somewhat similar for these new *Eptatretus* species, but there are significant differences in the multicusps, numbers of gill pouches, and prebranchial slime pores which readily distinguish each of them. Some differences are found in the white patterns on the face and barbels of the seven pigmented specimens (Fig. 2), but color cannot be assigned major importance as a species character with such a small sample size.

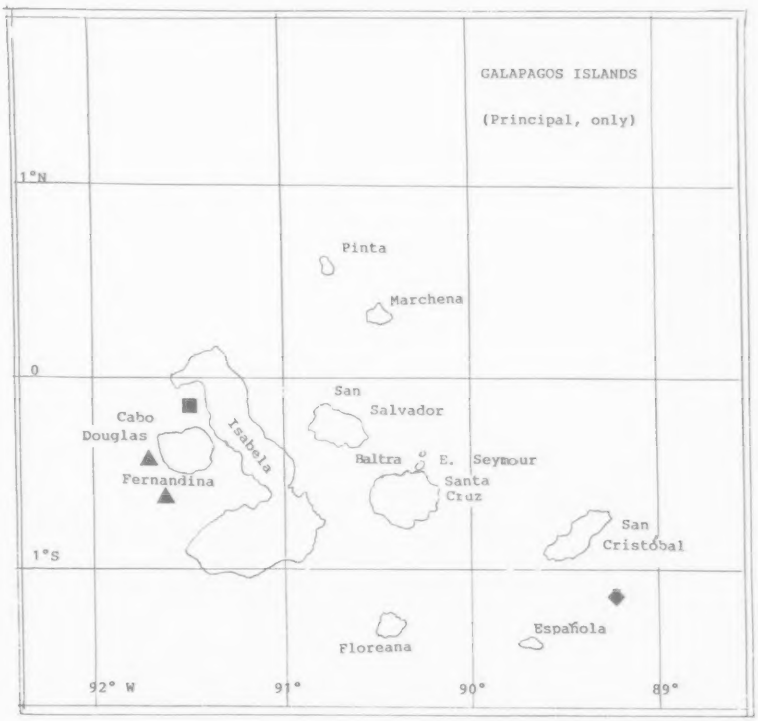

Figure 1

Principal islands of the Galápagos Archipelago, showing collection locations of the three new species of *Eptatretus*: ■ = *E. grouseri*; ◆ = *E mccoskeri*; and ▲ = *E. wisneri*.

Material and methods

All new specimens for this study were collected by John E. McCosker et al using the research submersible *Johnson Sea-link* (JSL), on the California Academy of Sciences and Harbor Branch Oceanographic Institute Galápagos Expedition during November 1995. The three new species collected by the California Academy of Sciences and described below were among eight specimens taken in four trap sets; additional specimens (nontypes) of Galápagos *Eptatretus* were given to the Instituto Nacionál de Pesca, Guayaquil, Ecuador, and were not available for study. Collection data and disposition of specimens are listed in the treatment of each new species. Institutions in which type specimens have been deposited are the California Academy of Sciences, San Francisco (CAS), United States National Museum, Washington, D.C. (USNM), and Scripps Institution of Oceanography, La Jolla, California (SIO).

McCosker[1] described the method of capture as follows: "Hagfish were collected with a small, galvanized wire commercial two-fyked minnow trap, about 30 by 50 cm, with 2 cm openings at each end. The traps were baited with fish or molluscs, or both, weighted and set with a pinger and short float line to be retrieved on the next dive [about 8 h later]; all traps were set among boulders, often on steep slopes." McCosker further reported that every set resulted in hagfish so elusive that many escaped traps during or after retrieval. Hagfish were also seen, but not taken, at 267 m off East Seymour Island, at 274 m off Isla Floreana (Charles Island), and off Isla San Salvador (James Island) at 884 m over sand bottom, at 6.54°C. Although no study material resulted from these sets, the reports furnish information on the little-known habitat of these benthic fish and indicate locations for further collecting effort.

Methods of measuring and counting follow those of McMillan and Wisner (1984) and Wisner and McMillan (1995). Counts of gill pouches (GP), gill apertures (GA), and cusps are noted for both sides, but body proportions and slime pore counts are for the left side only. Low power magnification was required to discern head grooves and fusion of multicusps. Most of the specimens are twisted and previously cut, making some measurements and counts difficult; all specimens were measured several times and averages

[1] McCosker, J. E. 1996. California Academy of Sciences, Golden Gate Park, San Francisco, CA , 94118-4599. Personal commun.

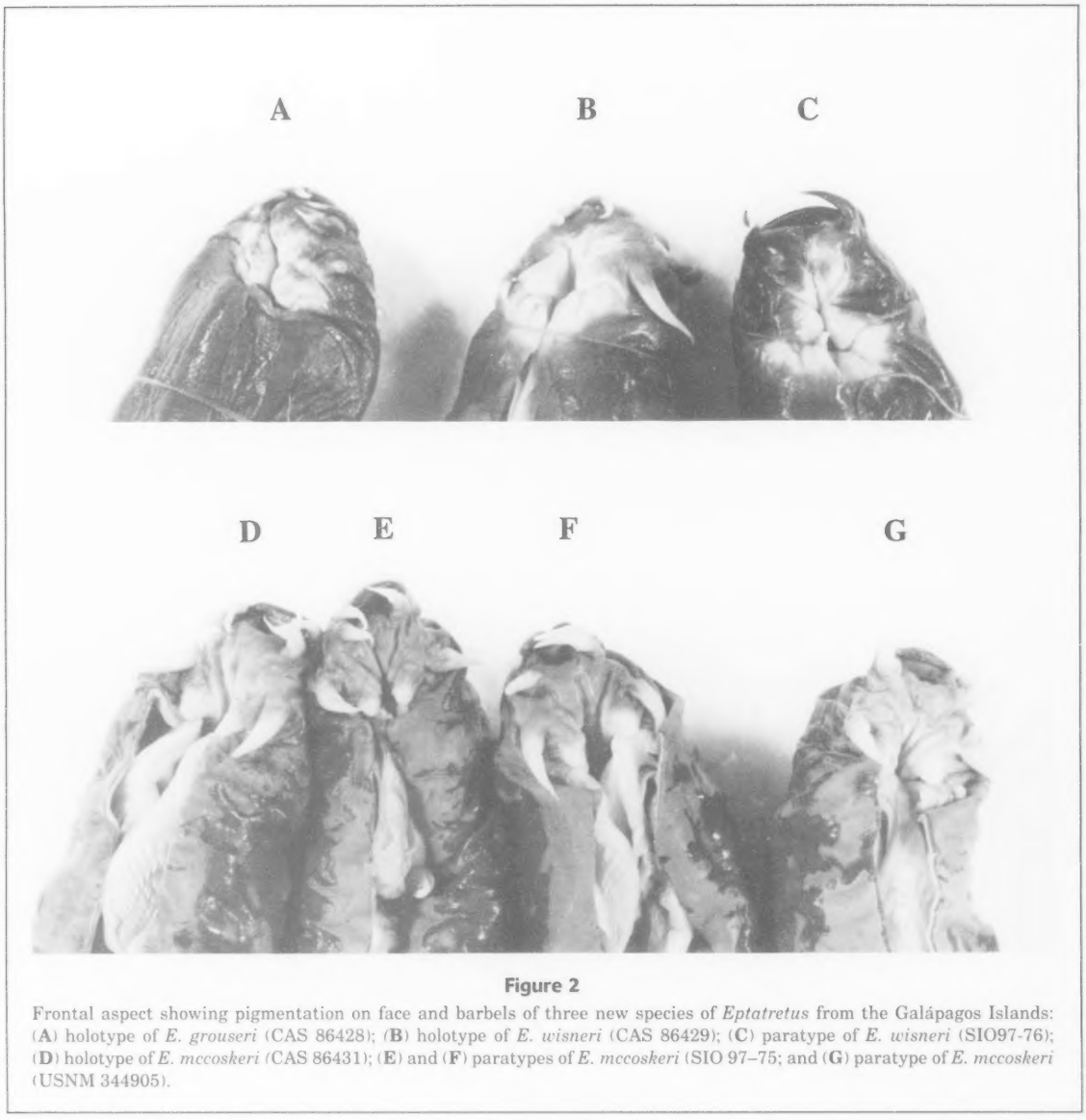

Figure 2

Frontal aspect showing pigmentation on face and barbels of three new species of *Eptatretus* from the Galápagos Islands: (**A**) holotype of *E. grouseri* (CAS 86428); (**B**) holotype of *E. wisneri* (CAS 86429); (**C**) paratype of *E. wisneri* (SIO97-76); (**D**) holotype of *E. mccoskeri* (CAS 86431); (**E**) and (**F**) paratypes of *E. mccoskeri* (SIO 97–75; and (**G**) paratype of *E. mccoskeri* (USNM 344905).

used to calculate body proportions in thousandths of total length (TL). About 6–9 mm of shrinkage was noted in the total lengths of the seven larger specimens between 24 March 1996 and 20 March 1997. Some shrinkage occurs in all specimens on preservation, mainly in the trunk length, and apparently slightly more when ethanol is the preservative used, as in this case. Selected body proportions and counts of slime pores and cusps are shown in Table 1.

Because variations in color patterns are often noted in large collections, color is not usually considered of much importance. However, the two species with eight gills have distinct differences in the white patterns on their faces and barbels that may provide a useful character in distinguishing between them. The "face" is the anteriormost part of the specimen, the ventral aspect of the head, delineated by three pairs of long, slender protruberances thought to be sensory organs and commonly referred to as barbels. The first two pairs are above and below and adjacent to the nasopharyngeal duct, which is the intake opening for water to the pharynx.

The third pair lies just outside another set of short, fleshy protruberances on each side of the mouth,

Table 1

Selected measurements and counts of slime pores and cusps of three new species of *Eptatretus* from the Galápagos Islands. Species name followed by number of specimens in parentheses; total length of holotype followed by TL of paratype(s) in parentheses; body proportions in thousandths of TL, average followed by values for all specimens.

Measurements	*E. grouseri* (2)	*E. mccoskeri* (4)	*E. wisneri* (2)
Total length in mm	380 (142)	320 (283,298,300)	360 (328)
Prebranchial length	225 (211–239)	249 (237–262)	213 (194–229)
Branchial length	71 (63–79)	97 (93–101)	105 (100–111)
Trunk length	544 (535–553)	494 (487–500)	516 (503–28)
Tail length	160 (158–162)	162 (156–177)	168 (167–171)
Body depth withVFF	58 (49–68)	100 (94–106)	88 (85,92)
Body depth without VFF	54 (42–66)	100 (94–106)	87 (85–89)
Body depth at cloaca	54 (48–61)	83 (78–88)	72 (72–73)
Tail depth	63 (63–63)	93 (87–102)	77 (76–78)
Slime pore counts (holotypye followed by paratype(s) in parentheses):			
Prebranchial pores	12 (13)	15 (14,14,14)	9 (9)
Branchial pores	4 (5)	7 (7,7,7)	7 (7)
Trunk pores	46 (44)	42 (40,40,41)	46 (47)
Tail pores	15 (14)	10 (10,11,12)	14 (13)
Total pores	77 (76)	74 (72,72,74)	76 (76)
Cusp counts, left, right (holotype followed by paratype(s) in parentheses:			
Multicusps, ant./post.	3,3/2,2	3,3/3,3	3,3/2,2
Unicusps(anterior rows)	8,9 (9,9)	10,10[a](9,9–9,10)	9,9 (9,9)
Unicusps(posterior rows)	8,8 (8,8)	9,10 (9,9–9,10)	8,8 (8,8)
Total cusps	44 (44)	51 (48,50,51)	44 (44)

called "labial barbels," which are immediately adjacent to the oral opening, very similar in size and shape in all hagfish, and are not considered species signifcant. The other three pairs of long, slender barbels are usually measured, and sometimes used as a species character. Because many of the barbels on these specimens were curled and accurate measurements difficult to repeat, this character has not been included in Table 1. Multicusp pattern, and counts of GP and slime pores have proved to be more accurate and less variable intraspecifically than color or barbel size, and thus more important as species characters. The most significant features of taxonomic importance in this study are the counts of gill pouches, prebranchial slime pores, and multicusps. "First" and "last" refer to anteriormost and posteriormost, and tail pore counts are the sum of cloacal and caudal slime pores; other terms used are from Wisner and McMillan (1990, 1995). The water passes from the the nasopharygeal duct through the pharynx, through each afferent branchial duct (ABD) to the gill pouch, and exits through each efferent branchial duct (EBD) to its corresponding external opening (GA). Any excess water passes out of the body through the slightly larger duct known as the pharyngocutaneous duct (PCD), which is ordinarily confluent with, or occasionally just posterior to the last GP on the left side. The numbers of gill apertures are not shown in the table because the number of GA is normally the same as that of GP in the genus *Eptatretus*; however, GA count is given in each species description and in the key because the apertures are readily counted by external examination and thus provide a useful character for identification in the field. In most *Eptatretus,* including the three species described in the present study, the number of branchial pores is one less than the number of gill apertures,and each pore is slightly below and posterior to each GA anterior to the PCD. The next slime pore, usually found above and behind the PCD, is the first in the trunk pore series.

Key to the species of *Eptatretus* of the Galápagos Islands

1a Five or six gill pouches and apertures each side; multicusps 10 (3 in each anterior row and 2 in each posterior row) total cusps 44; prebranchial slime pores 12–13, trunk pores 44–46, tail pores 14–15, total pores 76–77 ..... ***E. grouseri*, new species**

1b Eight gill pouches and apertures each side **2**

2a Prebranchial slime pores 14–15, trunk pores 40–42, tail pores 10–12; total pores 72–74, total cusps 48–51, multicusps 12 (3 in each row); nasal barbels completely white; face mostly dark with a small white area around mouth and on labial barbels ..... ***E. mccoskeri*, new species**

2b Prebranchial slime pores 9; trunk pores 46–47, tail pores 13–14; total pores 76, total cusps 44, multicusps 10 (3 in anterior, 2 in posterior rows), nasal barbels dark with occasional white tips; face, mouth, and base of labial barbels nearly all white ..... ***E. wisneri*, new species**

Eptatretus grouseri new species

Holotype CAS 86428, female, 378 mm TL, taken at 00°14.6'S, 91°26.6'W, in a minnow trap at 2370 ft [722 m], 17 November 1995.

Paratype SIO97-77 (formerly CAS 86428), 142 mm TL, (juvenile, sex not determined), taken with the holotype.

Diagnosis Five or six gill pouches and apertures each side, last GA confluent with PCD on left side. Multicusps 3 in anterior and 2 in posterior rows, 9 unicusps in each anterior and 8 in each posterior row, total cusps 44; slime pore counts: prebranchial 12–13, branchial 4–5, trunk 44–46, tail 14–15, total slime pores 76–77; ventral finfold (VFF) vestigial, caudal finfold (CFF) well developed.

Description Both specimens have a bluntly rounded rostrum; barbels well developed, first two pairs about equal, third pair slightly longer; greatest body depth in trunk region about the same as tail depth, both only about 6 to 7 percent of TL; prebranchial length about 23 percent of TL, trunk length about 54 percent of TL. Although the two specimens differ greatly in size and color, counts of pores and cusps are very similar (Table 1). The holotype has tiny round eggs less than one mm in diameter, no ellipsoidal developing eggs and no tissue indicating previous large eggs. Body color brownish-black, head region dark brown; eye spots prominent, nearly round; face dark with small white area around mouth and on tips of barbels (Fig. 2A); VFF vestigial, with pale margin on posterior third; cloacal opening white; GA widely spaced with branchial slime pores posterior to and just slightly below each aperture; all GA on the right side and all but the second on the left side have white margins. The second gill pouch on the right side of the holotype is either undeveloped or degenerated; it appears only as thickened muscle tissue connecting the ABD from the pharynx with the EBD leading to the external GA. Only one GP lies along the tip of the dental muscle; the branchial aorta splits after the fifth (last) GP.

The paratype has six normally rounded GP on each side, the first two along the dental muscle with the aorta branching after the fifth GP. Possibly an albino, this tiny specimen is an unusual ivory to light tan body color, the prebranchial area slightly lighter with eye spots barely discernible. Also, the area around the mouth and cloaca are lighter than the body; the trunk region is just dark enough to show a white margin on the VFF. The slime pore openings are very small, but easily detected because the sacs bulge just under the thin skin.

The specimen is so young that it was not possible to determine gender even with magnification. The total cusp count only differs from that of the holotype by one, but they are very small and the multicusp fusion pattern is too indistinct to discern the number of fused cusps in the posterior rows with any certainty.

Etymology This species is dedicated to my son David "Grouser" McMillan, a Chief Engineer in the U.S. Merchant Marine, for his continued encouragement of my hagfish studies and for his knowledge and love of ships and the sea.

Distribution Known only from Galápagos Islands, Ecuador; both specimens were collected in JSL dive 3958 at 2370 ft [722 m] in Bolivar Channel, off Cabo Douglas, in a minnow trap set on a steep, sediment-laden slope of an invertebrate-rich pinnacle of pillow lava. This was the deepest set in which hagfish were collected on this expedition (Fig. 1).

Comments The body proportions differ by about two percent in prebranchial length and depth of body in trunk region, possibly because one specimen is a juvenile. Pore and cusp counts, which remain the same throughout the individual's life span, are very similar in both specimens. In this tiny paratype the first GP is about 3.5 mm in diameter, with each subsequent GP decreasing in size posteriorly until the sixth is only about 2 mm across. This difference has also been noted in size of unicusps, in which the last one is frequently much smaller at the end of each row, apparently a normal growth pattern. I have not made any study of changes in body proportions of hagfishes from juvenile to adult stage because very small specimens are seldom collected. The capture of this tiny

specimen was possible because of the use of a minnow trap with very small openings. Because of the larger openings of the myxinid traps most often used, hagfishes of less than 200 mm length are seldom caught because they escape before a trap reaches the surface.

The larger specimen with normal pigmentation has been designated as the holotype (in spite of its one abnormal GP), because its adult size allowed determination of gender and multicusp pattern, as well as more accurate measurements and slime pore counts. These two specimens are assigned to the same species because there is such close agreement in cusp and slime pore counts and most body proportion and because they were collected in the same JSL dive. A difference of one gill pouch is common in large collections of *Eptatretus* having nine or more GP, and this difference may be found occasionally in species having only five or six gill pouches. More specimens will be required to determine the usual number of GP, and whether there are enough other differences to warrant separating into two different species.

Discussion Three species of five- or six-gilled *Eptatretus* from the Caribbean Sea are *E. minor* and *E. multidens* Fernholm and Hubbs (1981), and *E. mendozai* Hensley (1985). Although these three species may have once shared a common ancestor with *E. grouseri*, they are readily distinguished by their unusual 3/3 multicusp pattern (three fused cusps on both the anterior and posterior rows of cusps). The 3/2 multicusp pattern of *E. grouseri* commonly occurs in most species of *Eptatretus:* two other five-gilled species with this pattern are *E. profundis* (Barnard, 1923) from South Africa and *E. eos* Fernholm (1991) from the Tasman Sea, the latter a distinctive pink color and possessing a tube-shaped, elongated "snout." Both of these species have about 26 prebranchial slime pores, an unusually high number for *Eptatretus* and twice as many as found in *E. grouseri.* Four species of *Eptatretus* with six gill pouches and the 3/2 multicusp pattern are *E. burgeri* (Girard, 1854) from Japan and Korea, *E. hexatrema* Barnard (1923) from South Africa, *E. longipinnis* Strahan (1975) from South Australia, and *E. chinensis* Kuo and Mok (1994) from the South China Sea. *Eptatretus burgeri* has a distinctive white middorsal line as well as notably higher prebranchial and total slime pore counts, whereas the other three species have prebranchial pore counts two to three times that of *E. grouseri.* Although the number of GP is the same, these six species are not considered closely related to *E. grouseri* because of the significant differences in prebranchial and total slime pore counts, as well as wide geographic separation.

***Eptatretus mccoskeri* new species**

Holotype CAS 86431, male, 320 mm TL, taken at 01°06.3'S, 89°06.9'W, in a minnow trap at 704 ft [215 m], 16 Nov 1995.

Paratypes All males, taken with the holotype; SIO97-75, 2(283,300 mm TL); and USNM 344905, 298 mm TL.

Diagnosis Eight gill pouches and apertures each side, last GA confluent with the PCD on the left side; 12 multicusps (3 fused cusps in each row), unicusps 36–39 (9,9 to 10,10 unicusps in each anterior and 9,9 to 9,10 in each posterior row), total cusps 48–51; total slime pores 72–74, prebranchial 14–15, branchial 7, trunk 40–42, tail 10–12. Ventral finfold absent or vestigial; caudal finfold with white margin; head slightly lighter than body color, face dark except for small white area around mouth; barbels all white (Fig. 2, D–G).

Description Body color brownish black with head region slightly lighter than body color, face dark except for small white area around the mouth; eye spots visible, but not prominent; face dark, in sharp contrast to completely white barbels; prominent white margin around CFF; rostrum bluntly rounded, nearly straight across; nasal orifice large, face wide with the distance between the pairs of barbels about equal to that of their length. First five (4–6) GP lie along the dental muscle; branchial aorta branches at the sixth or seventh GP; first GA high, series curving downward to the PCD near the ventral midline; series of prebranchial slime pores starts far forward; branchial pores are tiny and close to ventroposterior margins of each GA, trunk pore series starts above and behind the PCD, a space about 5–6 mm between last trunk pore and origin of cloaca. Prebranchial length is about one fourth of TL, trunk length about half of TL; greatest body depth in the trunk region about equal to the tail depth, both about 10 percent of TL (Table 1).

Etymology This species is dedicated to my friend John E. McCosker, Senior Scientist, California Academy of Sciences, San Francisco, California, for providing this new study material, as well as for his important contributions to marine biology.

Distribution Known only from the Galápagos Islands, Ecuador; all four specimens were taken in one dive (JSL 3936) from a minnow trap set on sand bottom at the top of a seamount southeast of Isla San Cristobal (Chatham Island) at about 215 m, the shal-

lowest set where hagfish were found on this expedition (Fig. 1).

Comments Because male hagfish rarely outnumber females in any collection, it is unusual to find that these four specimens are all males; testes are developed, but no study was done to determine presence of sperm. Although both *E. mccoskeri* and *E. wisneri* (described below) have eight GP, the pattern of three fused cusps in both anterior and posterior rows, notably higher numbers of prebranchial pores and total cusps, and the sharp contrast of white barbels against the dark face of *E. mccoskeri* readily distinguish these two species. Also, the prominent white margin around the entire caudal finfold in *E. mccoskeri* is much less apparent in *E. wisneri,* showing only as a thin white edge on the tip of the CFF. The numbers of pouches along the dental muscle and position of branching of the branchial aorta also differ slightly in these two 8-gilled species. Three other species of *Eptatretus* with 8 GP and the 3/2 multicusp pattern are listed below in the discussiom of *E. wisneri.*

Eptatretus wisneri new species

Holotype CAS 86429, female, 356 mm.TL, taken at 00°28.0'S, 91°37.2'W, from a minnow trap at 1848 ft [563 m], 14 Nov 1995, [JSL dive 3952].

Paratype SIO97-76 [formerly CAS 86430], male, 328 mm TL, taken at 00°17.5'S, 91°38.9'W, from a minnow trap at 1680 ft [512 m], 16 Nov, 1995 [JSL dive 3957].

Diagnosis Eight gills and apertures on each side, last GA on left side confluent with PCD; 10 multicusps, pattern of 3 fused cusps in each anterior row and 2 in each posterior row; unicusps 9 each anterior row and 8 each posterior row; total cusps 44; total slime pores 76, prebranchial pores 9, branchial pores 7, trunk pores 46–47, tail pores 13–14; face mostly white, including mouth and base of labial barbels; other barbels dark, with occasional white spots or tips (Fig. 2, B and C); eye spots distinct, large and irregularly shaped; VFF vestigial or absent, CFF well developed.

Description Body color brownish-black, head slightly lighter, with large, distinct eye spots; gill apertures with white margins; face nearly all white, including area around mouth and base of labial barbels; the VFF appears only as a pale line on the posterior half of the trunk region and the tip of the CFF has a thin pale margin. The first 3 gill pouches lie along the dental muscle; the branchial aorta branches after fifth GP; the prebranchial length is about 21 percent of TL, trunk length about half of TL, the greatest body depth in trunk region about equal to, or slightly more than the tail depth, both about 8 to 9 percent of TL (Table 1).

Etymology This species is named after Robert L. Wisner, my friend and associate at Scripps Institution of Oceanography, for his invaluable assistance with my myxinid research as well as his other contributions to ichthyology.

Distribution Known only from Galápagos Islands, Ecuador, these two specimens were taken by minnow trap on two different JSL dives, off Cabo Douglas, Isla Fernandina (Narborough Island), at 512 and 563 meters (Fig. 1).

Comments The holotye is a young female with round eggs of less than one mm, with no ellipsoidal oocytes and without evidence of tissue indicating previous vitellogenesis. The paratype is a male with well-developed testes, but no examination was done for the presence of sperm. One specimen is more brown than black, and the white face patterns are slightly different; also, the barbels of one specimen are partly white and more robust than those of the other (Fig. 2, B and C). These slight differences could be due to gender, although pigmentation is highly variable and sexual dimorphism has not been reported in hagfish. Barbels are seldom used as a species character because they are often curled, making accurate measurements difficult, and not reliable as a body proportion because their lengths are so small compared with TL. These two specimens have the same pattern of multicusps and unicusp counts, and slime pore counts are the same or only differ by one. Therefore, until further collecting provides more specimens for comparison, the slight differences in pigmentation patterns and size of barbels are considered insignificant, and the two specimens are described as one species.

Discussion *Eptatretus wisneri* is readily distinguished from *E. mccoskeri* because of its multicusp pattern of 3/2 (three on each anterior and two on each posterior row), lower numbers of total cusps, notably lower number of prebranchial and total slime pores, as well as the darker barbels and the white areas over most of the face. Three other eight-gilled *Eptatretus* with the 3/2 multicusp pattern are *E. octatrema* Barnard (1923) from South Africa, *E. indrambarayai* Wongratana (1983) from the Andaman Sea (N.E. Indian Ocean), and *E. okinoseanus* (Dean, 1904) from Japan). However, they are not con-

sidered closely related to *E. wisneri* because of differences in counts, the wide geographical separation, and the fact that this multicusp pattern is common to most species of *Eptatretus*.

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Chemical marking of juvenile snapper, *Pagrus auratus* (Sparidae), by incorporation of strontium into dorsal spines

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Abstract.—The aim of this project was to investigate the use of strontium as a chemical tag in the dorsal spines of the marine teleost *Pagrus auratus* that would allow the mass tagging of juvenile fish. Previous studies in which the incorporation of strontium has been experimentally manipulated for the purposes of marking have generally concentrated on freshwater and anadromous species. This is the first study to investigate the tagging of spines with strontium, the removal of which is nondestructive. Inductively coupled plasma-mass spectrometry (ICP-MS) was used to measure isotopic concentrations. The dorsal spines of juvenile *P. auratus* that had been immersed in salt water containing 0.125 g/L $SrCl_2 \cdot 6H_2O$ (5× ambient strontium) and 0.250 g/L (10× ambient) for five days incorporated ^{86}Sr at levels greater than those in control fish. The strontium signal was persistent in spines for at least 36 days and showed no sign of decay during the experiment. No effects of the treatments on fish health or growth were detected. Short-term immersion experiments (6 hours to 5 days) indicated that treatments of 10× ambient or greater for 4–5 days were required to tag fish reliably with strontium. Natural levels of strontium in the spines of juveniles varied among locations separated by tens of kilometres along the coast of New South Wales. Natural variations in strontium concentrations were not great enough, however, to obscure the differences between tagged and wild fish. It was concluded that strontium immersion is a useful and relatively environmentally safe method of tagging large numbers of small fish.

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Calcium is incorporated into the calcium carbonate matrix of otoliths and into the calcium phosphate matrix of the skeleton, spines, and scales as fish grow (Francillon-Vieillot et al., 1990). In addition to calcium, trace elements, such as strontium, are also incorporated into the calcified components of fish. The chemical similarities of Ca^{2+} and Sr^{2+} ions (i.e. similar ionic radius and identical valence) allow strontium ions to act as replacements for calcium during the process of calcification. Ca and Sr concentrations in calcified components have been explored for their relationships with variations in environmental conditions (Edmonds et al., 1989; Gallahar and Kingsford, 1992), such as temperature (Kalish, 1989; Radtke et al., 1990; Townsend et al., 1992, 1995) and salinity (Kalish, 1990; Coutant and Chen, 1993; Secor et al., 1995).

The manipulation of ambient levels of chemicals such as strontium can allow fish to be marked or tagged invisibly. The marking of skeletal structures with isotopes offers a potential method for rapid tagging of large numbers of small juvenile fish. Nonradioactive strontium has been investigated, and artificially induced strontium marks have been detected in otoliths (Brown and Harris, 1995; Mugiya and Satoh, 1995; Mugiya and Tanaka, 1995; Schroder et al., 1995, 1996; Gallahar and Kingsford, 1996), scales (Ophel and Judd, 1968; Behrens-Yamada and Mulligan, 1982; Snyder et al., 1992), vertebrae (Behrens-Yamada et al., 1979; Behrens-Yamada and Mulligan, 1982, 1987; Schroder et al., 1995), and opercular bones (Guillou and de la Noue, 1987; Schroder et al., 1995). The majority of this work, however, has been done on freshwater or anadromous species.

The species investigated in this study was the snapper or red sea bream, *Pagrus auratus* (Pisces; Sparidae). The northern hemisphere and southern hemisphere forms (previously *Pagrus major* and *Chrysophrys auratus*, respectively) are now considered to be morphometrically identical (Paulin, 1990). This highly valued commercial species supports a very well established intensive aquaculture industry in Japan (Foscarini, 1988; Davy, 1990, 1991; Fukusho, 1991) and shows good potential for aquaculture in

Australia and New Zealand (Battaglene and Bell, 1991; O'Sullivan, 1992; Treadwell et al.[1]). Commercial catch rates of snapper have been on the decline in many areas (Paul, 1982; Gilbert, 1986), and one means of increasing natural populations is by reseeding the sea with hatchery-reared larvae or juveniles. *Pagrus auratus* is one of the targets for this approach in both the northern (Smith and Hataya, 1982; Ishibasi, 1986; Matsuda, 1992) and southern (Smith and Francis[2]) hemispheres. Tagging techniques are required to measure the success of such stock enhancement measures. Very large numbers of small juveniles must be tagged in these studies, and isotope tagging may be one of the more suitable techniques.

Tagging techniques have been extensively used for research on *Pagrus auratus*. Studies involving tagging have been used to investigate migration (Crossland, 1976; Jones, 1981; Sakamoto, 1984; Kato et al., 1991), the identification of separate stocks (Sanders, 1974; Moran, 1987), growth rates (Sanders and Powell, 1979; Francis and Winstanley, 1989; Tsukamoto et al., 1989; Kato et al., 1991), fishery exploitation and resilience (Crossland, 1980), and the validation of aging with oxytetracycline (Ferrell et al., 1992; Francis et al., 1992). With the exception of fluorochrome markers, such as oxytetracycline, many conventional tagging techniques are, however, unsuitable for tagging small juveniles or are too energy intensive or expensive for the tagging of large numbers of fish.

The objective of our study was to determine whether juvenile snapper (*Pagrus auratus*) could be reliably chemically tagged by the incorporation of strontium into the dorsal spines from immersion in strontium chloride. The specific aims were as follows: 1) to investigate the persistence of chemical tags in the dorsal spines of juvenile snapper following immersion of the fish in strontium chloride; 2) to determine minimum strontium concentrations and immersion periods required for effective strontium tagging; 3) to determine the feasibility of batch tagging with different levels of strontium; and 4) to compare the levels of strontium in tagged snapper with naturally occurring levels in wild-caught snapper from different estuaries. These multiple controls were required to ensure that natural variation did not confound the identification of treated fish.

Methods

Experimental work was carried out at the New South Wales (NSW) Fisheries Brackish Water Fish Culture Research Station (BWFCRS), Port Stephens. The experimental fish were hatched on 13 November 1993 from wild parent snapper caught off Broughton Island, NSW. Rearing procedures and larval characteristics may be found in Fukuhara (1985), Lopez (1986), Pankhurst et al. (1991), Battaglene and Talbot (1992), and Kingsford and Atkinson (1994). Experimental fish were kept in 2000-litre tanks on a constant flowthrough system of biofiltered oceanic water for the first three weeks, followed by biofiltered estuarine water from Salamander Bay, Port Stephens. From 14 January 1994, 770 juvenile snapper were reserved for the experiments.

The strontium salt used was strontium chloride ($SrCl_2 \cdot 6H_2O$), a relatively cheap, nontoxic and nonradioactive chemical. Strontium is found naturally in seawater at an elemental concentration of approximately 8.1 mg/L (Horne, 1969). For simplicity the amounts of strontium chloride added to the saltwater experimental tanks are expressed as multiples of this ambient strontium concentration, as follows: 1) Sr^{2+} five times ambient = 0.125 g/L of $SrCl_2 \cdot 6H_2O$; 2) Sr^{2+} ten times ambient = 0.250 g/L of $SrCl_2 \cdot 6H_2O$; and 3) Sr^{2+} forty times ambient = 1.000 g/L of $SrCl_2 \cdot 6H_2O$. Preliminary experiments (Pollard[3]) showed increased levels of dorsal spine strontium in juvenile snapper that had been immersed in strontium chloride solution.

Experiment 1: persistence of strontium

The aim of this experiment was to determine whether the strontium marks induced in the dorsal spines of juvenile snapper were persistent over at least a 36-day period. The experiment was initiated on 22 March 1994 when the fish were 129 days old and 68 mm mean fork length (SD ±6.7 mm). The experiment consisted of Sr^{2+} five times ambient, Sr^{2+} ten times ambient, and a control, each with four replicate 100-litre tanks containing eight fish each. Two fish were sampled from each tank at zero, 12, 24, and 36 days following the termination of the five-day exposure period. For comparisons between sample times, treatments, and tanks we used a partially hierarchical three-way analysis of variance.

[1] Treadwell, R., L. McKelvie, and G. B. Maguire. 1992. Potential for Australian Aquaculture. Research Report 92.2 of the Aust. Bureau of Agricultural and Resource Economics, Canberra, Australia, 81 p.

[2] Smith, P. J., and M. P. Francis. 1991. Snapper reseeding in the Hauraki Gulf: scientific considerations. N.Z. MAF Fisheries Internal Report 172, Wellington, New Zealand, 22 p.

[3] Pollard, M. J. 1994. Chemical marking of juvenile snapper (*Pagrus auratus;* Sparidae) by the incorporation of iron and strontium in the spines, scales and otoliths. B.Sc. Hons. thesis, School of Biological Sciences, Univ. Sydney, Sydney, Australia, 119 p.

It was possible that Sr could affect fish growth. Thus, the change in mean fish weight per tank between the initial stocking of the tanks and the sampling of the fish remaining after 36 days was compared between treatments by using one-way analysis of variance.

Experiment 2: concentration and exposure period

The aim of this experiment was to investigate a range of strontium treatments and exposure periods in order to determine minimum concentrations and times required for marking the dorsal spines of juvenile snapper. It was also possible that different batches could be identified by different levels of strontium incorporation.

The experiment was initiated on 3 March 1994 when the fish were 110 days old and 64 mm mean fork length (SD ±4.1 mm). The 16 treatments comprised three strontium concentrations (Sr^{2+} five times, ten times, and forty times ambient) matched with each of five exposure periods (6, 12, 24, 36, and 48 hours) and a control treatment. Replication comprised two 100 litre tanks per treatment, each containing six fish. Snapper were sampled seven days after the termination of the chemical treatment. Statistical analysis involved comparisons between treatment concentrations, exposure periods, and tanks using an asymmetrical design analysis of variance and the Student-Newman-Keuls (SNK) multiple range test.

Strontium levels in wild fish

Juvenile *P. auratus* were caught between November 1993 and April 1994 with Opera House fish traps (100 × 80 × 60 cm, stretched mesh size 11 mm) from each of four estuarine locations around the Sydney region. From each estuary 20 fish of similar size to those used in experiments one and two were selected: those from Botany Bay had a mean fork length of 63 mm (SD ±5.9), from Port Jackson, 80 mm (SD ±9.9), from Middle Harbour, 82 mm (SD ±4.4), and from Port Hacking, 80 mm (SD ±5.6).

The main aim of this experiment was to compare naturally occurring levels of dorsal spine strontium in wild-caught juvenile snapper from multiple locations, of potentially different water chemistries, with 1) snapper immersed in Sr 40× ambient for 48 hours, and 2) snapper immersed in Sr 10× ambient for 5 days. Statistical analysis involved one-way analysis of variance and the SNK multiple range test.

Treatment of experimental fish

The experiments were undertaken in an enclosed room containing thirty-two cylindrical 100-litre fibreglass tanks, each with a 500-µm mesh filter, an aquarium air stone and a clear plastic cover. Twice daily water exchange from Salamander Bay was provided by a 1000-litre supply tank for each row of eight tanks. Photoperiod was ten hours of light per day, and tanks were cleaned weekly. Approximately 0.125 g of feed per fish per day was distributed in three equal portions throughout the day. The specially formulated dry snapper diet was a 50% protein extruded diet based on 64% fish meal, similar in composition to that in Quartararo et al. (1992). To maintain a constant stocking density, fish mortalities were compensated for by replacement with similar-size untreated snapper, fin-clipped for identification.

The water quality parameters measured every second day were pH (which averaged approximately 8.1), electrical conductivity (approx. 52 mS/cm), turbidity (generally 0 or 1 NTU), dissolved oxygen (approx. 8.6 mg/L), water temperature (approx. 19–23°C), and salinity (approx. 34.3 ppt). No significant differences were observed between tanks for any of these parameters, which remained within a range generally acceptable for the maintenance of fish health (Poxton and Allouse, 1982).

Treatments were randomly allocated to tanks. All fish chosen appeared healthy and in good condition. Wet weight and fork length were measured prior to introduction of representative groups to the experimental tanks. Sedation was necessary to allow safe handling and was achieved with 0.5 mL/L of benzocaine solution, which comprised 100 g/L ethyl p-amino benzoate ($C_9H_{11}NO_2$) in 70% ethanol solvent (Summerfelt and Smith, 1990). The fish were acclimatized to the tanks for a period of 5 days for experiment 1 and 8 days for experiment 2. Strontium treatments were initiated by dissolving the appropriate quantity of chemical salt in each tank. For the duration of the treatment there was no water exchange or cleaning activities. There was also no feeding of the fish during treatment to avoid uneven uptake of the chemical marker among individuals as a result of differential feeding (e.g. Gallahar and Kingsford, 1996). Treatment was terminated after the prescribed exposure period by allowing the exchange of new water. Fish were removed by dip net from the tanks and placed into a lethal dose of 1.0 mL/L benzocaine solution at the appropriate time of sampling, then measured, and frozen for storage.

Dorsal spine tissue samples were dissected from the treated and control snapper. Each sample consisted of four sturdy spines from the midfront of the dorsal row. The weaker posterior spines were avoided where possible. These samples were then placed into polypropylene eppendorf tubes and dried overnight in a 75°C oven. The tubes were then cooled for half

an hour prior to weighing. The tubes were sealed during this time to reduce moisture uptake which could have caused an increase in weight. Samples were weighed to the nearest 0.001 mg.

The remaining steps took place in a laminar flow cabinet to avoid contamination. With a pipette we placed 50 µL of 1% nitric acid (H_2NO_3) into the eppendorf tube containing the spines for 10 seconds and then removed the acid. This procedure cleaned possible external contaminants from the surface of the sample. The time and concentration needed for cleaning were determined by microscopic examination of the spines to check for excessive etching and loss of bone. The contents of the eppendorf tube were then dissolved in a proportional amount of 75% nitric acid to produce a standard 1 mg of spine tissue per 10 µL of solution. After allowing an hour or more for the sample to fully dissolve in the sealed tube, 10 µL of solution was removed and added to a sample tube containing 4950 µL of milliQ water and 40 µL of concentrated nitric acid. This resulted in a standardized 0.2 mg/µL sample solution in 1% nitric acid which became the sample concentration used in our experiment after preliminary analyses with ICP-MS.

Table 1

Analysis of variance for experiment 1: persistence over 36 days. Three-way partially hierarchical analysis of variance to test for differences in dorsal spine ^{86}Sr among sample times 0, 12, 24, and 36 days (fixed factor=time), treatments (treat) (Sr^{2+} zero, 5× and 10× ambient; fixed factor), and tanks (random factor). Nonsignificance at P=0.05 is indicated by n.s. Cochran's test; df = 1; no. variances (k) = 48; and C = 0.1565; variances homogeneous; no transformation.

Source	df	Mean square	F-ratio	Probability
Time	3	13699.2	6.690	<0.005
Treatment	2	568635.5	105.485	<0.001
Time × treat	6	4536.0	2.215	n.s.
Tanks (treat)	9	5390.7	2.632	<0.050
Time × tanks (treat)	27	2047.8	0.695	n.s.
Residual	48	2946.5		

Measurement of isotopes

Inductively coupled plasma-mass spectrometry (ICP-MS) was used to measure concentrations of strontium in the dorsal spine tissue. The model used was a Perkin-Elmer SCIEX ELAN 5000 with a Gilson 212B autosampler for sample introduction, and procedures were similar to those described in Dove et. al. (1996). The ICP-MS was optimized with a 0.010 mg/L standard solution covering the extremes of the mass range. By using the graphics application, we were able to adjust the nebulizer flow to maximize the ^{103}Rh signal and balance the signals for ^{24}Mg and ^{208}Pb from the standard solution. The quantitative analysis function of the ICP-MS was externally calibrated by using calibration standards with concentrations of 1, 10, 100, and 500 parts per billion, i.e. those covering the range of expected concentrations. The correlation coefficient of the calibration curve was generally 1.000 for ^{86}Sr, the isotope used for analysis. ICP-MS interferences such as isobaric overlaps or plasma-induced polyatomic ions are generally negligible for strontium. A blank solution containing only the 1% nitric acid matrix was also analyzed prior to the sample solutions, so that the isotopic concentration of the acid matrix could be subtracted.

Quality control solutions were analyzed for ^{86}Sr at the start, middle, and end of each analytical run for each date of analysis, allowing the stability of the analyte signal to be monitored both within and between runs. The quality control readings obtained were not constant over time, owing perhaps to clogged sampling cones. The results for the spine samples, therefore, required adjustment in relation to the quality control results. We assumed that there was no change in the ^{86}Sr concentration of the quality control solution over time. External drift correction can significantly improve both accuracy and precision (Jarvis et al., 1992).

Treatment of data

Data were analyzed by analysis of variance according to the general recommendations of Underwood (1981). Normality of data was tested with Cochran's test. Student-Newman-Keuls (SNK) multiple range tests were used for *a posteriori* comparisons among treatments where appropriate. Where data were missing (<2 per design), the missing values were replaced by the means for their group, and the degrees of freedom of the residual were reduced by the number of missing values.

Results

Persistence of strontium over 36 days

Differences in the ^{86}Sr concentrations of dorsal spines were found among treatments, despite differences among tanks within treatments (Table 1; Fig. 1). Fish exposed to strontium at 10× ambient incorporated more strontium into their spines than fish at 5×

ambient (SNK: Control<Sr 5× <Sr 10×). Slight fluctuations, particularly in the control and Sr 10× ambient treatments (Fig.1), caused significant differences to be found between some sampling times (Table 1), however these were not picked up by the less sensitive SNK test (0 days=36 days=12 days=24 days). The ranks of different treatments remained similar irrespective of sample time (i.e. no sample time × treatment interaction) and there was no indication of a significant decay of the strontium signal over the 36 days of the experiment. There were no significant differences between tanks within each treatment.

There were no significant differences observed among treatments for the growth of snapper as measured by the change in mean wet weight per tank between the initial stocking and sampling at 36 days (ANOVA: df=2, 9; F=3.27; P=0.086, n.s.). Mortality rates were also very low for all treatments. These results suggested that effects on health or growth from the immersion of fish in strontium were minimal.

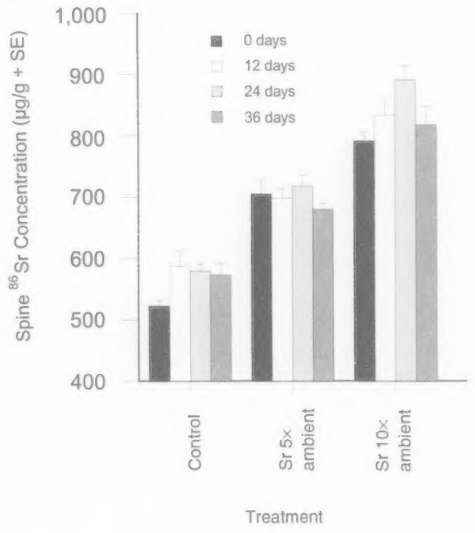

Figure 1

Persistence over 36 days of ^{86}Sr in the spines of juvenile snapper immersed in zero, 5× ambient and 10× ambient strontium for 5 days.

Table 2

Analysis of variance for experiment 2: asymmetrical design analysis of variance to test for differences in spine ^{86}Sr incorporation among treatment concentrations (conc.) (Sr^{2+} 5×, 10× and 40× ambient; fixed factor), exposure periods (exp.) (6–48 hours; random factor), and tanks (random factor). Nonsignificance at P=0.05 is indicated by n.s. Cochran's test: degrees of freedom (df) = 5; no. of variances (k) = 32; C = 0.1329; variances homogeneous; no transformation.

Source	df	Mean square	F-ratio	Probability
Concentration	2	1005648	18.167	<0.01
Exposure period	4	204047.2	163.683	<0.01
Conc. × exp.	8	55355.9	44.405	<0.01
Tanks (conc. × exp.)	15	1246.6	0.575	n.s.
Control vs. rest	1	237036.4	190.146	<0.01
Residual	150	2166.3		

Strontium concentration and exposure period

^{86}Sr was incorporated rapidly into the dorsal spines of treated snapper and on average the concentrations were significantly higher in treated fish than in controls (Table 2; Fig. 2). Significant differences were found among groups of snapper treated with different $SrCl_2$ concentrations, and the magnitude of these differences varied with exposure period, resulting in a significant concentration × exposure period interaction (Table 2). Strontium incorporation increased as the exposure period increased, and the magnitude of this change was also not equal between treatments. The signals from the Sr 40× treatment were generally much greater than either of the Sr 5× or Sr 10× treatments, which were similar to one another, and the Sr 40× signal also increased much more rapidly between exposure periods (Fig. 2).

Strontium in wild fish

The experimental snapper immersed in Sr 10× for 5 days and Sr 40× for 48 hours had spine ^{86}Sr concentrations higher than those of any of the control groups (ANOVA: df=6, 105; F=70.9; P<0.001; Fig. 3), with respective concentrations 1.37 (mean 833 µg/g) and 1.55 (942 µg/g) times greater than the maximum mean concentrations of any wild fish (Port Hacking; 607 µg/g).

There were also significant differences between estuaries of origin of the wild-caught fish (ANOVA: df= 3, 74; F= 5.8; P < 0.01; Fig. 3). Fish from Botany Bay had lower levels of strontium than those from the other estuaries (SNK: Botany Bay<Port Jackson=Middle Harbour=Port Hacking). There was a 102 µg/g difference in mean spine strontium between the highest and the lowest estuary of origin. Fish from Port Jackson and Middle Harbour had intermediate values that were similar to one another. The fish used as controls during the experimental period at Port Stephens also

had similar concentrations to the wild-caught control fish.

Discussion

Persistence of strontium

Fish that were chemically tagged with strontium could be distinguished from control fish, and the chemical marks were persistent for at least 36 days, showing no decrease and no regular pattern of change. Although in practice the length of a tagging experiment would be likely to exceed this time frame, persistence over 36 days may indicate that the strontium signal is also likely to persist over longer periods. This conjecture, however, remains to be validated and may be dependent on factors such as bone metabolism and growth. Artificially induced strontium signals in fish scales (Ophel and Judd, 1968) and otoliths (Brown and Harris, 1995; Schroder et al., 1995, 1996) have been shown to be detectable for periods of greater than a year, and other studies investigating these components have also shown successful strontium incorporation (Table 3).

Scales (Lapi and Mulligan, 1981) and otoliths (Edmonds et al., 1989) are relatively metabolically inert tissues, and there is little biological reworking of trace elements deposited within them. On the other hand, the living cells of bone tissue may be metabolically active during growth and there may be some turnover of material over the long term. This bone remodeling is related to morphogenesis and physiological factors and involves a balance between bone resorption and bone redeposition (Francillon-Veillot et al., 1990). Nevertheless, it is likely that spines are fairly inert components of the skeleton and that active resorption is unlikely to be high, indicated by the ability to age some fish by the growth rings in spines (e.g. McFarlane and Beamish, 1987; Brennan and Cailliet, 1989; Welch et al., 1993). In addition, similar chemical processes of strontium incorporation during calcification exist between scales, otoliths, and bone, and it was expected that the incorporation of strontium into the spines would result in a relatively constant mark.

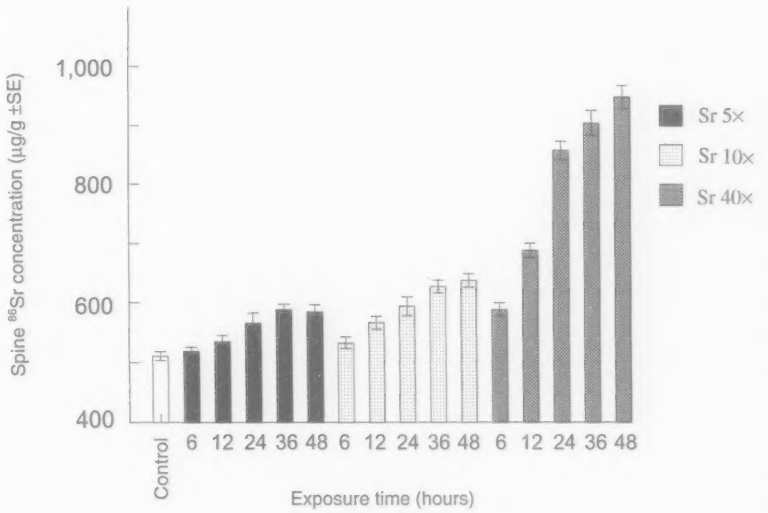

Figure 2

Differences in ^{86}Sr incorporation into the spines of juvenile snapper treated with different immersion concentrations and exposure periods.

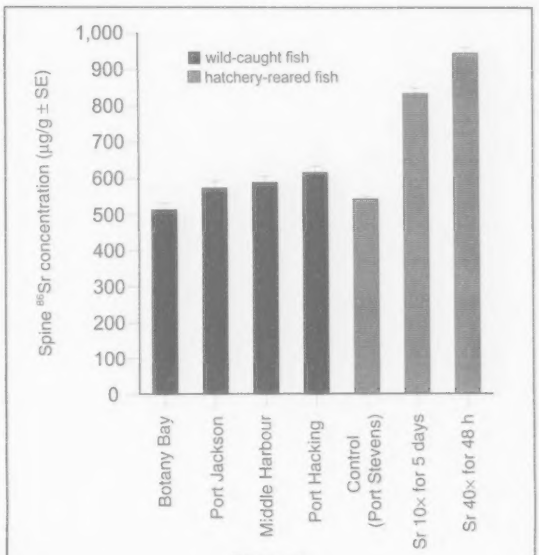

Figure 3

Naturally occurring levels of ^{86}Sr in the spines of wild *Pagrus auratus* from four estuaries in New South Wales, Australia, compared wirh those of hatchery-reared fish (controls from Port Stephens, N.S.W.) and fish treated with strontium.

Behrens-Yamada et al. (1979) found that strontium appears to become metabolically inert in the vertebrae of coho salmon, *Oncorhynchus kisutch*, after

Table 3

Comparison of previous literature in which nonradioactive strontium was incorporated into the tissues of fish for the purposes of chemical marking.

Reference	Species investigated	Aquatic medium	Method of administration	Skeletal structure	Effectiveness
This study	snapper juveniles (*Pagrus auratus*)	saltwater	immersion in 0.125g/L to 1.0 g/L Sr^{2+} (5 to 40× ambient) for 6 h to 5 days	dorsal spines	Strontium levels of greater than 10× ambient for 4–5 days produced marks which could be reliably distinguished from controls and wild snapper.
Ophel and Judd (1968)	goldfish (*Carassius auratus*)	freshwater	32 g of strontium lactate per 400 g of wet diet	scales	More than 10 times the levels of Sr in controls after one year.
Behrens-Yamada et al. (1979)	coho salmon (*Oncorhynchus kisutch*)	freshwater treatment, released into saltwater	10,000 ppm Sr introduced through the diet over 60 days	vertebrae	32 times as much Sr as controls when released; 1.4 times as much in jacks after 5 months; adults could not be distinguished.
Behrens-Yamada and Mulligan (1982)	coho salmon adults	as above	as above	core samples of scales and vertebrae	Successful identification of adults after 5 months.
Behrens-Yamada and Mulligan (1987)	coho salmon fry	freshwater	immersion in 1 µg/mL Sr for 49 days	vertebrae	Sr mark still detectable after 169 days despite dilution.
Guillou and de la Noue (1987)	brook trout (*Salvelinus fontinalis*)	freshwater	200–3200 µg/g Sr^{2+} introduced through the diet for 4 and 6 weeks	opercular bones	Able to distinguish between marked and unmarked fish at the lowest levels of ingested Sr.
Snyder et al. (1992)	rainbow trout (*Oncorhynchus mykiss*)	freshwater	immersion in 1.8, 3.6 and 5.4 mg/L Sr for 30 days and 60 days	scales	A twofold increase in exposure period and a two- or threefold increase in immersion concentration produced corresponding two- and threefold increases in incorporation.
Brown and Harris (1995)	golden perch (*Macquaria ambigua*) and trout cod (*Maccullochella macquariensis*)	freshwater	immersion in 1–20 g/L $SrCl_2$ for one to four days	otoliths	Still able to distinguish after 12 months. No measurable growth, health, or mortality effects.
Mugiya and Tanaka (1995)	goldfish (*Carassius auratus*)	freshwater	immersion in 0.1, 1.0, and 10.0 mg/L Sr for 88 days	otoliths, ribs, and scales	Strontium in otoliths remained after 92 days, whereas that in scales and ribs decreased.
Schroder et al. (1995)	chum (*Oncorhynchus keta*) and sockeye salmon (*O. nerka*) fry	freshwater	immersion in 120, 1200 and 9000 ppm $SrCl_2$ for 24 hours	otoliths, vertebrae and opercula	Able to distinguish after 34 days, and after 21 months in otoliths of fish immersed in 5000 ppm for 24 hours.
Schroder et al. (1996)	salmon fry	freshwater	immersion in 9000 ppm $SrCl_2$ for 12 hours or less	otoliths	Fish held for as little as 30 minutes in 9000 ppm were distinguishable for up to 2 years.
Gallahar and Kingsford (1996)	rock blackfish (*Girella elevata*)	saltwater	immersion in $SrCl_2$ 2.5× ambient	otoliths	Able to distinguish between marked fish and controls.

incorporation. Their inability to identify strontium-marked adults in following years was attributed entirely to dilution caused by the growth of vertebrae, rather than a process of leaching from the tissue. Behrens-Yamada and Mulligan (1982) found that the use of smaller vertebral core samples allowed the identification of strontium-labelled adult salmon. The limiting core diameter was related to the vertebral diameter of the juvenile salmon at the time of treatment.

Similarly, the growth of juvenile snapper spines will cause a dilution of the strontium signal. The ratio of marked to unmarked spine matrix will decrease as the spine enlarges. Spine growth occurs from the base upwards (e.g. McFarlane and Beamish, 1987), and the strontium mark may remain only in the upper regions as spine elongation and enlargement occurs. Only the uppermost section of the spine, corresponding to the length of the spine at the age of incorporation, should be sampled in large fish; this will result in a proportional increase in the amount of strontium in the sample.

Papadopoulou et al. (1980) found that a range of chemical constituents in the otoliths of the mackerel *Scomber japonicus colias* decreased with age. Dilution from growth, dietary changes with age, and otolith compositional changes were mentioned as possible causes. Nevertheless, the duration of most tagging experiments does not generally exceed a period of several years, and growth or age-related problems are unlikely to be a major concern over such time scales. The differences between the strontium-tagged and wild fish are great enough for there to be little confusion between the two groups if samples are taken from the uppermost spine region and tagging experiments are not designed to extend over the very long term.

Strontium in tagged and wild fish

It was a major concern for our study that naturally occurring variation in the levels of strontium in wild fish might obscure the strontium signal in fish that had been tagged by immersion in $SrCl_2$. Adult snapper may undertake movements associated with feeding or spawning (Crossland, 1976), extending the range of water chemistries experienced by the fish. Moreover, juveniles may remain resident in shallow bays and estuaries that are subject to variable inputs of fresh water (Kingsford and Suthers, 1994) and that are likely to have differences in water chemistry.

Despite the observed variation in natural levels of strontium in wild snapper, the treatments with Sr 10× for 5 days (Fig. 3) and Sr 40× for 24 to 48 hours (Figs. 2 and 3) had unequivocally higher readings. Other treatments also had higher readings. They were, however, not considered great enough for effective tagging owing to the increased variation in spine strontium expected to result from growth factors and exposure to the variable marine environment. The minimum concentration recommended is Sr^{2+} 10× ambient, with an exposure period of at least 4–5 days at this concentration. Shorter exposure periods will require concentrations greater than Sr 10×, and snapper significantly larger than those used in our study may also require higher treatment concentrations. Although the comparisons were made with wild snapper captured within a period of six months in the general region of Sydney across a range of less than 40 km of coastline, it is unlikely that fish tagged with strontium at this recommended level would be confused with wild fish from any latitude or time.

It is not surprising to find differences in naturally occurring strontium among fish from different estuaries. For example, Edmonds et al. (1989) investigated eight elements, including strontium and found elemental compositions to be specific to the geographical origin of nonmixing populations of snapper in Western Australia. Similarly, Port Jackson, Botany Bay, and Port Hacking are distinct estuaries which would also be expected to contain nonmixing juvenile snapper populations. On the other hand, Middle Harbour is within Port Jackson, and interestingly no significant difference has been observed between these two groups.

A variety of factors influence natural variation in the Sr content of otoliths. Salinity is perhaps the strongest determinant, and analysis of strontium levels has long been used to interpret the salinity histories of anadromous or catadromous fish species (Castonguay and Fitzgerald, 1982; Coutant and Chen, 1993; Limburg, 1995; Secor et al., 1995; Pender and Griffin, 1996). Decreasing water temperature causes an increase in otolith Sr/Ca ratio, with the greatest effect occurring at low temperatures. This knowledge has been used in attempts to reconstruct temperature histories of wild fish (Radtke and Targett, 1984; Radtke et al., 1990; Townsend et al., 1989, 1992, 1995, Arai et al., 1996). It has been suggested that low temperatures may impair physiological mechanisms that exist in fish and inhibit the uptake of strontium (Kalish 1989; Townsend et al., 1992). Other environmental and biological factors that influence the natural markings of calcified structures include pH (Moreau et al., 1983; Wickins, 1984), fish age and size (Papadopoulou et al., 1980; Gauldie et al., 1995), developmental and reproductive events (Francis, 1994; Kingsford and Atkinson, 1994), physiology (Kalish, 1991), periods of stress (Townsend et al., 1992), dietary differences (Edmonds et al., 1989;

Limburg, 1995; Gallahar and Kingsford, 1996), and anthropogenic pollutants (Kalish, 1995). All of these factors may cause variation in levels of strontium in wild fish. Hence, if strontium tagging is to be successful in a region, the magnitude of natural variation should be investigated at appropriate spatial and temporal scales.

Strontium tagging has been used for freshwater and anadromous species (Table 3), but investigations of saltwater species are limited. Hurley et al. (1985) marked the statoliths of the short-finned squid *Illex illecebrosus* and Gallahar and Kingsford (1996) marked the rock blackfish *Girella elevata*. Because seawater has some 200–400 times the strontium content of freshwater (Guillou and de la Noue, 1987), the range of concentrations available for tagging (i.e. before saturation and precipitation) is reduced for marine fish. This limited our ability to batch mark separate groups of fish with different concentrations of the same element, especially considering the unknown factors affecting long-term persistence, such as dilution due to growth. Multiple immersions in strontium have, however, created multiple, discrete bands on the otoliths of salmon, allowing the production of codes for batch marking (Schroder et al., 1996). Another attractive possibility is to mark batches of fish with different combinations of several elements. A characteristic of ICP-MS analysis is the ease in identification of a number of isotopes with little corresponding increase in preparation time. Schroder et al. (1996) found that rubidium was incorporated into the calcified tissues of juvenile salmon. Caesium, which has a similar ionic radius and the same +2 valence as calcium, may also prove to be a likely candidate for consideration. Pollard[3] investigated iron chloride ($FeCl_3 \cdot 6H_2O$) together with strontium chloride, however the iron was not successfully incorporated into the dorsal spines of snapper.

Advantages, limitations, and applications of the technique

The strontium immersion technique allows hundreds of fish to be tagged in a single batch without the need for individual treatment. Other more labor intensive methods may introduce problems of stress from fish handling and are unsuitable for large numbers, especially the very large numbers involved in reseeding programs. Stock enhancement in Japanese waters exceeds 15 million juvenile snapper each year (Tsukamoto et al., 1989). Strontium tagging may be applied to very small fish and even larval fish (e.g. Behrens-Yamada and Mulligan, 1987). Fast body growth and the difficulties of attachment make the conventional tagging of small fish extremely difficult. Some alternatives to batch tagging with strontium and with comparable advantages include microwire tags (Beukers et al., 1995), thermal marking (Schroder et al., 1996), oxytetracycline (Francis et al., 1992; Lang and Buxton, 1993), alizarin complexone (Lang and Buxton, 1993; Secor and Houde, 1995) and other chemical fingerprints (e.g. Gillanders and Kingsford, 1996). It may be useful for some purposes to use a combination of techniques simultaneously.

The costs associated with the analysis of samples on ICP-MS are relatively high compared with those of many conventional tagging techniques, however they may compare favourably with the costs of some other chemical, electronic, or genetic methods of identification. The ICP-MS has very low detection limits, generally 100 to 1000 times more sensitive than inductively coupled plasma-atomic emission spectroscopy and inductively coupled plasma-atomic fluorescence spectrometry (Horlick and Shao, 1992). Sample preparation for ICP-MS is labor intensive; around 100 fish samples require up to 2 days preparation and a half day for analysis. Strontium marks however may also be detected by using other analytical techniques with lower costs, such as energy-dispersive x-ray spectrometry or wavelength dispersive spectrometry (Schroder et al., 1995). Many other analytical techniques, such as backscattered electron microscopy (e.g. Schroder et al., 1995), or laser ablation ICP-MS (e.g. Fowler et al., 1995), are also designed to measure microconstituents at specific loci across a section of calcified tissue, allowing the application of strontium marking for the validation of aging and batch marking of groups of fish.

Otoliths are commonly used for chemical marking and are the most widely used structures for age determination (Campana and Neilson, 1985). Otoliths comprise discrete, directly comparable samples and are recognized for their elemental stability (Edmonds et al., 1989). However, fish must be sacrificed for otolith sample collection. By contrast, spine and scale removal are nondestructive techniques, allowing catch and release techniques to be used for tagged fish. Spines are not shed or replaced during growth, unlike scales which may be lost, resorbed, or regenerated during fish ontogeny (Coutant and Chen, 1993). The small size of juvenile snapper scales also creates counting, weighing, and manipulation difficulties (Pollard[3]). The dissection of otoliths or other internal skeletal structures from large groups of fish is a labor intensive activity. The ease of removal of spines or scales allows for the routine sampling of these tissues regardless of the original purpose of fish collection. Removal for sampling could take place before the distribution of fish for commercial pur-

poses. Removal of spines or scales causes minimal physical defacement of the product, an aspect of particular relevance to the Japanese market where aesthetic appeal is highly valued.

The immersion technique for incorporation of strontium enables greater control over the degree of exposure of fish to strontium than does introduction through the diet. The latter method may introduce inconsistencies between experimental fish as a result of differential feeding, which often results from size hierarchies within the tanks (Umino et al., 1993). Intraperitoneal or intramuscular injection allows similar control of exposure to that of immersion; however each fish must be dealt with separately. Scott (1961) was unable to mark fish under 8 cm long by using injection techniques. Nevertheless, with large pelagic fish injection provides many advantages, including the ability to tag directly from the capture vessel.

The strontium tag showed no signs of decay due to leaching from the spine tissue, and tag retention times may prove to compare favorably with conventional methods. External physical tags are shed at different rates for different species, fish sizes, tag types, or attachment sites (e.g. Ingram, 1993), and may facilitate disease. Tattoos may be rendered unreadable by fish growth, and vital dyes may be leached from the animal (Laird and Stott, 1978). Clipped fins may regenerate, or there may be confusion between clipped fins and fins that have been naturally excised by predators. Population studies also assume that the proportion of tagged to untagged fish captured is representative of that existing in the population. These assumptions hold for strontium marking, whereas individuals marked with tags may be less fit for survival, more conspicuous to predators, or more likely to become entangled in capture nets.

Radioactive isotopes are effective markers of fish, as evidenced by the permanent marking of many fish by ^{14}C after atomic bomb testing in the 1950s (Kalish, 1995). A number of different radioactive isotopes have been investigated for fish tagging, for example ^{45}Ca (Bogoiavlenskaia, 1959; Anwand, 1966), ^{39}P (Karzinkin et al., 1959), ^{59}Fe (Scott, 1961), ^{137}Cs (Scott, 1962), ^{144}Ce (Hoss, 1967), ^{131}I (Fitzgerald and Keenleyside, 1978), ^{152}Eu and ^{155}Eu (Hansen and Fattah, 1986), ^{85}Sr (Carlson and Shealy, 1972; Lehtonen et al., 1992), ^{89}Sr (Farrell and Campana, 1996), and ^{90}Sr (Zhao et al., 1992). Marking with stable strontium salts however has many advantages over radioactive tagging, which is comparatively expensive, environmentally unattractive, and a potential threat to human health. The latter is an important criticism when radioisotope techniques are used to mark commercially important species, such as radioactive iridium used to tag and release snapper (Kato, 1990; Kato et al., 1991). Conversely, strontium immersion has in fact been suggested as a low-level marking technique for farm-reared brook trout destined for human consumption (Guillou and de la Noue, 1987).

A major disadvantage of the technique is that the existence of the strontium mark cannot be detected in recaptured fish prior to analysis. This means that large batches of snapper of the appropriate size may have to be analyzed when only a small proportion may be marked individuals. Most conventional tagging methods, including most radioactive isotope markers, allow *in vivo* detection of tagged fish. The number of fish requiring analysis should be minimized by the preselection of appropriate-size fish based on growth rate estimates for the appropriate geographic location (e.g. Francis and Winstanley, 1989; Tsukamoto et al., 1989; Paul, 1992). Moreover, other external features may also aid in the preselection of possibly marked fish; for example, a large proportion of hatchery-reared Japanese snapper lack an internostril epidermis (Sobajima et al., 1986). Salmon stocks of different origin have been identified by using naturally occurring differences in scale patterns (Bilton, 1972), otolith patterns (Hindar and Abee-Lund, 1992), vertebral elemental composition (Mulligan et al., 1983), or parasitic fauna (Margolis, 1963).

Stock enhancement or reseeding programmes may be of particular importance when there has been recruitment failure due to natural or anthropogenic environmental change, or as a result of overfishing. *Pagrus auratus* have been ranched and released for many years in Japan. Concerns have been raised about alterations to the gene pool from the introduction of genetically inferior cultured fish (Hindar et al., 1991; Harada, 1992). Smith and Hataya (1982) have however estimated that the release of one million snapper per year would increase annual net returns to the fishery by about 35 metric tons, and the Kagoshima Bay ranching operation appears to have become highly profitable (Matsuda, 1992). There has also been consideration of the establishment of snapper reseeding operations in the southern hemisphere (Smith and Francis[2]). Strontium tagging can assess the economic or conservation value of such stock enhancement operations and lead to refinement of the reseeding techniques, for example selection of the optimal locations and fish sizes for release. Consideration of migratory patterns (e.g. Crossland, 1976; Edmonds et al., 1989) is required to achieve spatial separation of studies, and temporal division of studies may also be achieved by the use of different cohorts separated by sufficient time to allow size separation. The success of the strontium immersion tech-

nique for *Pagrus auratus* indicates that it is probably applicable to many other saltwater fish species, and perhaps also to crustaceans and mollusks, but experimental validation would be required for each species.

Conclusions

The present study has demonstrated that the snapper *Pagrus auratus* can be reliably tagged by the incorporation of strontium into the dorsal spines. The use of strontium as a chemical marker can allow large numbers of small hatchery-bred fish to be tagged before release into the wild. Importantly, fish do not have to be sacrificed to assess whether they have been tagged. Strontium in the spines of snapper persisted for at least 36 days and there was no suggestion that the chemical signal decayed over this time. It is recommended that juvenile snapper require immersion in treatments of strontium chloride greater than 0.25 g/L (10× ambient) for 4 to 5 days for the production of reliable strontium marks in spines. Although natural levels of strontium in spines varied between some locations along the central coast of New South Wales, this variation was not great enough to obscure the differences between tagged and wild fish. It was concluded, therefore, that strontium immersion is a useful and relatively environmentally safe method of tagging large numbers of small snapper.

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Application of TOPEX-POSEIDON satellite altimetry to simulate transport dynamics of larvae of spiny lobster, *Panulirus marginatus*, in the Northwestern Hawaiian Islands, 1993–1996

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Abstract.—A commercially valuable trap fishery for spiny lobster (*Panulirus marginatus*) has existed in the Northwestern Hawaiian Islands since the late 1970s. Fisheries landings and research trapping show that spawning biomass and recruitment to the fishery collapsed in 1990 in the northern portion of the fishing ground and that there has been no recovery to the present, although recruitment remained strong at banks 670 km to the southeast. An advection-diffusion model is used to investigate larval transport dynamics between these two regions. The movement model is driven by geostrophic currents computed every 10 days from sea surface height obtained from TOPEX-POSEIDON satellite altimetry. The larval transport simulations indicate that even though larvae have a pelagic period of 12 months, banks differ substantially in the proportion of larvae they retain from resident spawners as well as the proportion of larvae they receive from other banks. In particular, recruitment to the northern portion of the fishing grounds is weak due to a very low local spawning biomass and a very limited contribution of larvae from the area of strong recruitment and high spawning biomass in the southeast. The results also suggest that satellite altimetry can provide useful information on physical dynamics for recruitment studies.

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The spiny lobster, *Panulirus marginatus*, is endemic to the Hawaiian Archipelago and Johnston Atoll. The species is found throughout the archipelago and is the target of a trap fishery in the northwestern portion of the archipelago known as the Northwestern Hawaiian Islands (NWHI). From the early 1980s to 1990, the majority of fishery catches came from two banks, Necker Island and Maro Reef, located 670 km northwest of Necker Island (Fig. 1). Catches during this period averaged about 60% from Maro Reef, 40% from Necker Island. However, in 1990 there was a dramatic collapse in recruitment of 3-year-old lobsters to the fishery at Maro Reef, and other banks north of Maro; this collapse has been attributed to climate-induced change in productivity that has impacted various other trophic levels, such as sea birds, monk seals, and reef fishes (Polovina et al., 1994). After the recruitment collapse, the fishery reduced the spawning biomass to very low levels at Maro and at other northern banks, and then fishing ceased in these areas. Even with the absence of fishing at Maro for at least six years, there is still no evidence of a recovery in recruitment as indicated from a time series of the relative abundance of 3-year-olds obtained from a standardized research survey (Fig. 2). However, at Necker, 670 nmi to the southeast, the recruitment drop at the end of the 1980s was much less severe and recovery has occurred in recent years and has supported a fishery (Fig. 2). The striking differences in recruitment levels over the past seven years between the two banks raises the possibility that there is limited larval mixing between the two banks.

Current management for the lobster fishery is based on the hypothesis that recruitment to the NWHI banks comes from a well-mixed pool of larvae with contributions from the entire archipelago, and this pool of larvae oscillates seasonally along the archipelago, pushed northwest in the spring and summer with tradewind-driven Ekman transport and pushed back southeast in the fall and winter with westerly wind-driven Ekman transport (MacDonald, 1986). A genetic analysis during 1978–80 examined allozyme variation in spiny lobsters from seven banks covering a substantial spatial range of the Hawaiian Archipelago and found no evidence of genetic differentiation between banks (Shaklee and Samollow, 1984). However, a subsequent study in 1987, using a

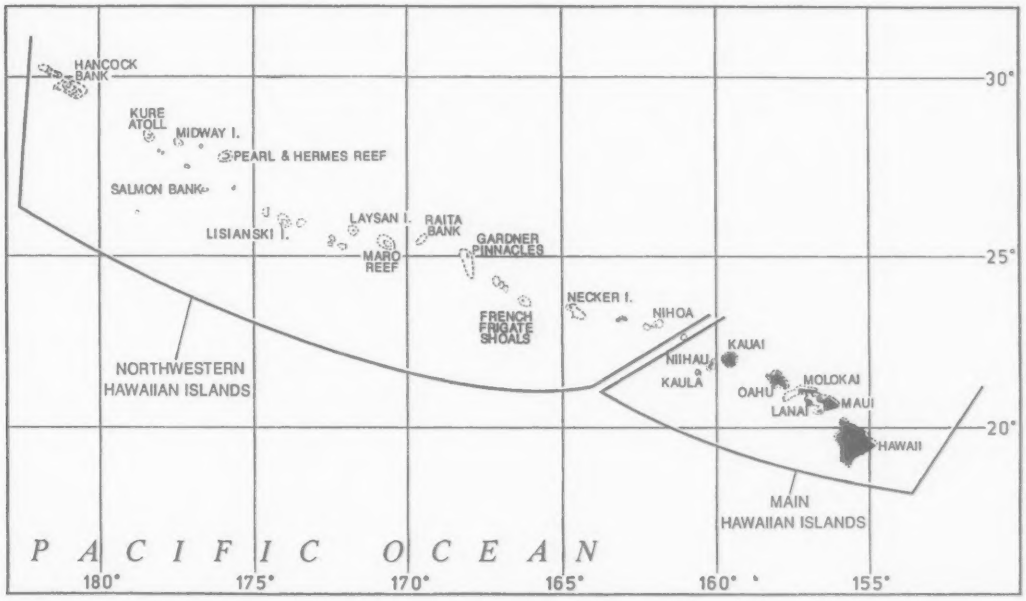

Figure 1
The Hawaiian Archipelago.

large sample size and comparing just Maro and Necker, found a statistically significant difference in allele frequency between Necker and Maro for one of the seven loci analyzed, raising the possibility that larval transport between the two banks may be limited (Seeb et. al., 1990).

The importance of Ekman transport in larval dynamics is not known, but larval sampling has found that a significant larval density exists well below the shallow Ekman layer and, in particular, that larvae appear to make diurnal movements from about 80–100 m in the day to 10–20 m at night (Polovina and Moffitt, 1995). Thus larval transport may be more influenced by transport of the mixed layer or geostrophic transport than by Ekman transport. The importance of geostrophic transport is also supported by correlations between sea-level height from tide gauges and spatial patterns in the subsequent fishery catches (Polovina and Mitchum, 1992, 1994). Indeed, the flat, leaf-like shape of spiny lobster larvae suggests they are adapted for passive horizontal transport assisted by vertical migration within the mixed layer (Lipcius and Cobb, 1994). The Hawaiian Archipelago lies near the center of the Subtropical Gyre; therefore the geostrophic transport consists of weak flow from northwest to southeast along the archipelago, turning to the east at the southern end of the archipelago. Although the mean geostrophic transport is weak, geostrophic mesoscale features, particularly eddies, are prevalent and are likely to be significant for larval spatial dynamics.

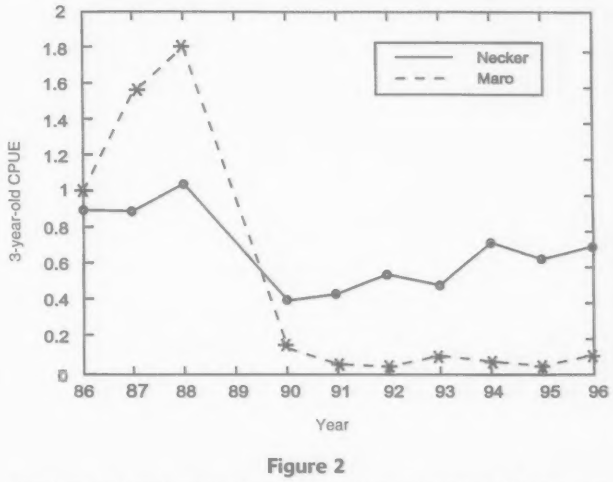

Figure 2
Standardized catch rates of age-3 spiny lobster (number of lobster per trap) from summer research cruises at Maro and Necker (data from Honolulu Laboratory, SWFSC, NMFS). No cruise conducted in 1989.

Since late 1992, data have been collected by TOPEX-POSEIDON (T-P) satellite altimetry and are available in near-real time. The satellite covers the ocean over a 10-day period, providing a temporal resolution of 10 days; however, the spatial coverage is along narrow tracks; therefore interpolation between track is required for full spatial coverage. We used this altimetry data to estimate geostrophic current and ultimately to drive a simulation model of the transport of spiny lobster larvae released from selected banks in order to describe the spatial and seasonal dynamics of larval transport. In particular, in the NWHI, the spiny lobsters spawn in the summer, during May–August, and in the winter, during November and December, and the larvae are estimated to have a pelagic duration of 12 months (Polovina and Moffitt, 1995). We investigated aspects of the spatial and temporal dynamics of spiny lobster larval transport by simulating the movement of larvae from several representative banks from summer and winter spawning over the 12-month larval duration.

Methods

Topex altimetry data

The altimetry data used in this study were obtained from a 2-day Delayed Altimeter Data project of the Laboratory for Satellite Altimetry, National Environmental Satellite, Data and Information Service (NESDIS), National Oceanic and Atmospheric Administration (NOAA), Department of Commerce. This project was a joint endeavor with the Naval Oceanographic Office (NOO) and the Jet Propulsion Laboratory (JPL). The altimetry data were first transmitted from the satellite to JPL, where the orbit position was finalized with the aid of GPS tracking data. NOO scientists performed an initial adjustment to the altimetry data using the JPL orbit information, then the data were forwarded to NOAA where a final orbit-related adjustment was made after the complete 10-day cycle of data was received. The data were aggregated into 1-degree latitude intervals along the satellite track (Fig. 3) and were expressed as a deviation from a 3-year (1993–95) mean altimetry. These data can be downloaded from an anonymous file transfer protocol (ftp) at

falcon.grdl.noaa.gov in/pub/topex_real_time

or from an internet webpage at

http://ibis.grdl.noaa.gov/SAT/near_rt/topex_2day.html.

The data were ready for public dissemination approximately 2 days after each 10-day satellite cycle was completed. Altimetry data that were not aggregated but were continuous along track lines are avail-

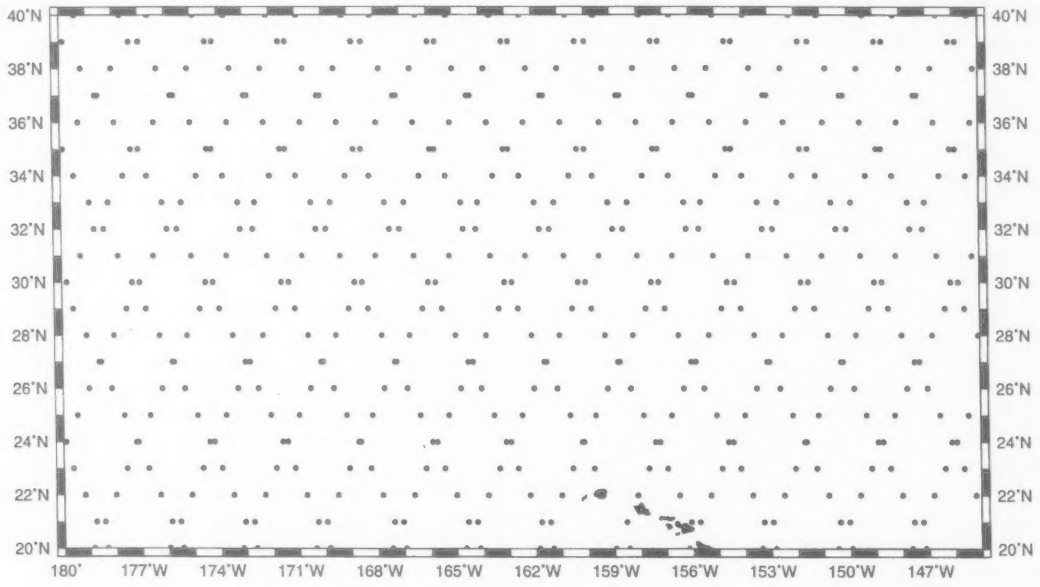

Figure 3
Spatial grid of near-real time TOPEX-POSEIDON data from a 10-day cycle.

able on CD-ROM from JPL. However, a considerable time lag may be associated with releases of these data.

After the data were downloaded, a unix shell script was used to process the individual cycle data. This script uses various subroutines of the Generic Mapping Tools (GMT) software package (the GMT software package is available from an anonymous ftp at kiawe.soest.hawaii.edu in /pub/gmt). The GMT script first smoothed and then interpolated the data using a subroutine called "nearneighbor." This subroutine placed the irregularly spaced track data onto a uniformly spaced latitude-longitude matrix, assigning values to each latitude-longitude location (node). Each node was assigned a weighted mean of all data points within a user-specified search radius (SR); i.e. a mean of all data within a geographic circle about each node. The weighting factor was a function of radial distance from the node such that $w(r) = 1/(1 + (3r/SR)^2)$, hence $w(r)$ ranged nonlinearly from 1 at the node (r=0) to 0.1 at SR units from the node (r=SR). When all orbital passes of the satellite cycle were complete, a SR value of 3 degrees could adequately interpolate regions between passes, independent of the relative date of the pass within the 10-day cycle, resulting in a complete grid file. For cycles with missing passes, the SR was able to be increased accordingly. The SR could also be specified as an absolute distance to ensure that the smoothing region was circular and not ovoid. After the deviation data were assembled on a grid, the script then added these data to another grid of equal dimensions containing the Levitus long-term mean dynamic height at 1000 m, which we assumed was representative of the mean dynamic topography for 1993–96. The Levitus data originated from the 1994 NODC World Ocean Atlas (CD-ROM data set), U.S. Department of Commerce, NOAA, National Environmental Satellite, Data, and Information Service (NESDIS). The grid file of absolute altimetry values (z) was then evaluated by the subroutine gridgradient, which calculates the east-west and north-south gradients, dz/dx and dz/dy, where x and y and z are all in centimeters. These gradients were used for calculating the u and v components of the geostrophic current as follows:

$$u = -(g/f)\frac{dz}{dy}$$

and (1)

$$v = (g/f)\frac{dz}{dx} ,$$

where g = 980 cm per second^2;
f = 2 Ω sin ϕ;
Ω = 7.29×10^{-5} radians per second (earth angular rotational velocity); and
ϕ = latitude.

These u and v values represent estimates at the surface. They can also serve as estimates of geostrophic current over the top 100-m mixed layer if integrals over the mixed layer of the horizontal density gradients are negligible. For the region of interest in our study, given the weak horizontal density gradients, the error in using these surface estimates as mixed layer estimates, according to calculations with the Levitus density field, was less than 2 cm/s. This is negligible given the time and space scales we were considering.

The u and v values were then output to an ASCII file at 0.5-degree resolution. A separate file for each 10-day period (n=169 from Oct 92 to Jun 97) was constructed for the entire Topex-Poseidon data set. The GMT script optionally produced a contour map of dynamic height with an overlay of geostrophic current vectors for each cycle. The resultant maps showed eddy and meander features that were likely important in recruitment processes (Fig. 4).

Several authors have found excellent agreement between currents estimated from T-P data and ground-truthing. Comparisons between the current estimated from satellite-tracked drogued buoys and geostrophic current estimated from T-P data in the western Pacific resulted in correlations of 0.924 for zonal velocity (u) and 0.760 for meridional velocity (v) (Yu et al., 1995). Comparisons between current speed from an acoustic Doppler current profiler along T-P track lines in the Hawaiian Archipelago agreed with estimates from T-P to within a few cm/sec (Mitchum, 1996). Sea surface height from T-P and a large set of island tide gauges, including those in the Hawaiian Archipelago, yielded a correlation of 0.66 (Mitchum, 1994).

Movement model

Individual larvae were tracked for a series of time steps starting from a given location by iteratively applying advective displacements due to water flow with additional random displacements caused by diffusion. The position of each larva was updated at each time step as follows:

$$x_{t+\Delta t} = x_t + \left[u_{(x_t, y_t, t)}\Delta t + \varepsilon\sqrt{D\Delta t}\right] / \cos(y_t) \quad (2)$$

$$y_{t+\Delta t} = y_t + \left[v_{(x_t, y_t, t)}\Delta t + \varepsilon\sqrt{D\Delta t}\right] ,$$

where t = time in days;

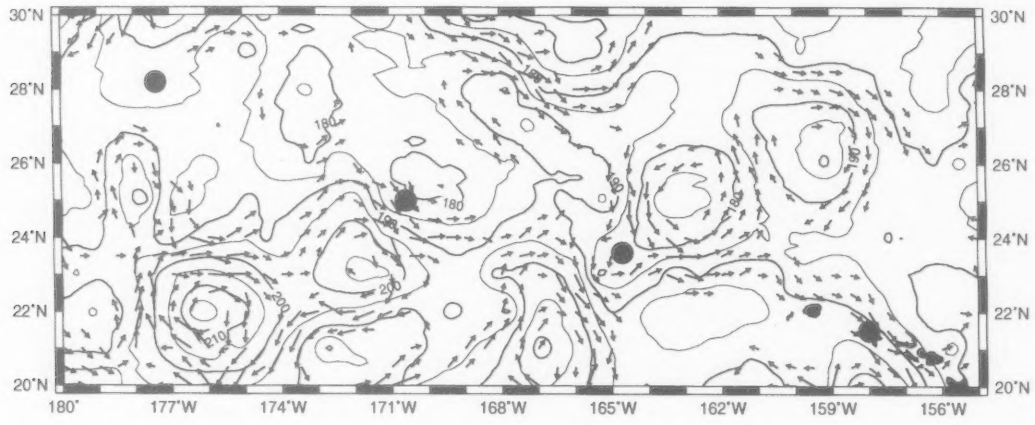

Figure 4

Sea surface height and geostrophic current estimated from a 10-day TOPEX/POSEIDON cycle, 16–26 August 1993. Only currents 8 cm/sec or larger are plotted with arrows. Solid circles from lower right (east) to upper left (west), denote Oahu, Necker, Maro, and Midway Islands, respectively.

x and y = the larval position in degrees of longitude and latitude respectively;
u and v = longitudinal and latitudinal components of velocity in degrees/day;
ε = a normal (mean 0, standard deviation 1) random variate; and
D = the eddy diffusion rate in units of degree^2/day (1 m^2/sec = 7×10^{-6} degree^2/day).

The first term in brackets in each equation is advective displacement and the second term, diffusional displacement. The cosine function in the longitudinal movement equation corrects for the fact that distance per degree of longitude decreases from the equator to the poles.

Values of u and v at particular locations and times were obtained by linear interpolation from the precalculated 0.5 degree by 10-day grid of u and v values computed from the T-P data. The time step was set to one day (Δt=1) with 365 iterations for one year of simulation. The 1-day time step was used to match the spatial resolution of the velocity field, but simulations showed that the choice of time step was robust up to about two weeks. Larvae dispersed in the model because a different diffusional displacement (a different ε) was chosen for each larva at each time step. Once larvae were even slightly separated, dispersal was further advanced because the larvae experienced different advective displacements as u and v varied spatially.

Simulations

Although lobsters presumably spawn on all banks in the Hawaiian Archipelago, for simplicity, the simulations released larvae from only four banks: Midway and Oahu (chosen as representative of the northwestern and southeastern ends of the archipelago) and Necker and Maro (representative of the main fishing banks [Fig. 1]). Each simulation released 5000 larvae at the beginning of the month from each of the four banks for the four months of the summer spawning season and the two months of the winter spawning season from 1993 to 1995. The simulations tracked the positions of all released larvae for 365 days; no larval mortality was assumed. For example, Figure 5 shows the distribution of simulated larvae 180 and 365 days after release at Maro Reef in July 1995. The distribution showed patchiness caused by underlying oceanographic features and expanded spatially over time. This simulation was based on an eddy diffusion rate of 1000 m^2/sec, and the same simulation, but with the diffusion rate reduced to 100 m^2/sec, showed a striking increase in patchiness and the same general dispersal (Fig. 6). The eddy diffusion rate for the NWHI is not known, but a range from 100 m^2/sec to 1000 m^2/sec has been proposed for another large archipelago, the Great Barrier Reef (Gabric and Parslow, 1994). Because the level of diffusion rate impacts larval patchiness and because we had a measure of actual larvae patchiness from numerous larval tows throughout the archipelago (Polovina and Moffitt, 1995), we decided the appropriate level for eddy diffusion rate by comparing the frequency distribution of larvae sampled in actual larval tows with the frequency distribution of larvae from line transects and the simulated spatial patterns for different eddy diffusion-rate values. The frequency distribution from transects with an eddy

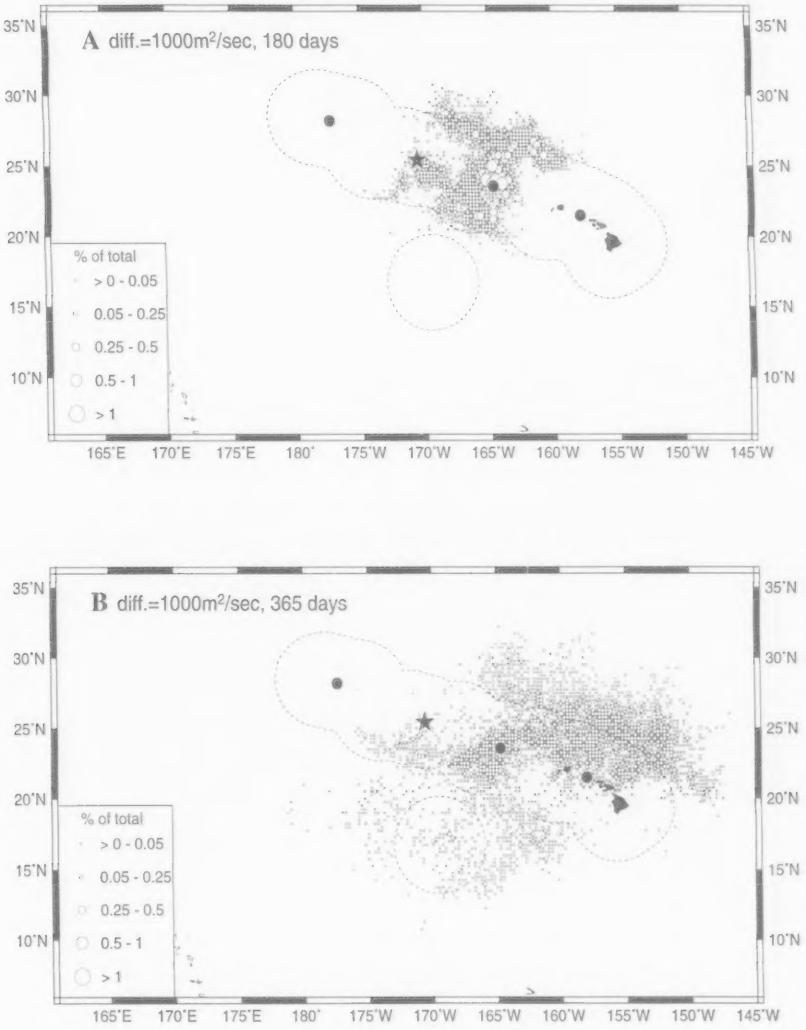

Figure 5

Simulated spatial distribution of 5000 larvae (**A**) 180 and (**B**) 365 days after release on 1 July 1995 at Maro with an eddy diffusion rate of 1000 m^2/sec. Solid circles denote Oahu, Necker, and Midway Islands, and the star marks Maro Island.

diffusion rate of 1000 m^2/sec had a lognormal distribution but underrepresented the heavy tails of the actual larval-tow frequency distribution. The frequency distribution from transects with an eddy diffusion rate of 100 m^2/sec had extremely heavy tails, in fact bimodal distribution. Either very few larvae were encountered or many larvae were encountered, resulting in a distribution that had too many large clumps compared with the observed distribution. However, an eddy diffusion rate of 500 m^2/sec produced a larval frequency distribution that closely matched the distribution from the larval tows, and this value was used in all subsequent simulations.

At the end of their larval period, spiny lobster larvae metamorphose into pueruli that, at least for other spiny lobster species, are capable of directed horizontal swimming over 40–60 km (Pearce and Phillips, 1994). For *P. marginatus*, it is not known how close a larva needs to be to a bank at the end of its larval period to recruit to that bank. The 200-m isobath around the islands and banks of the archipelago is generally circular and marks the points at

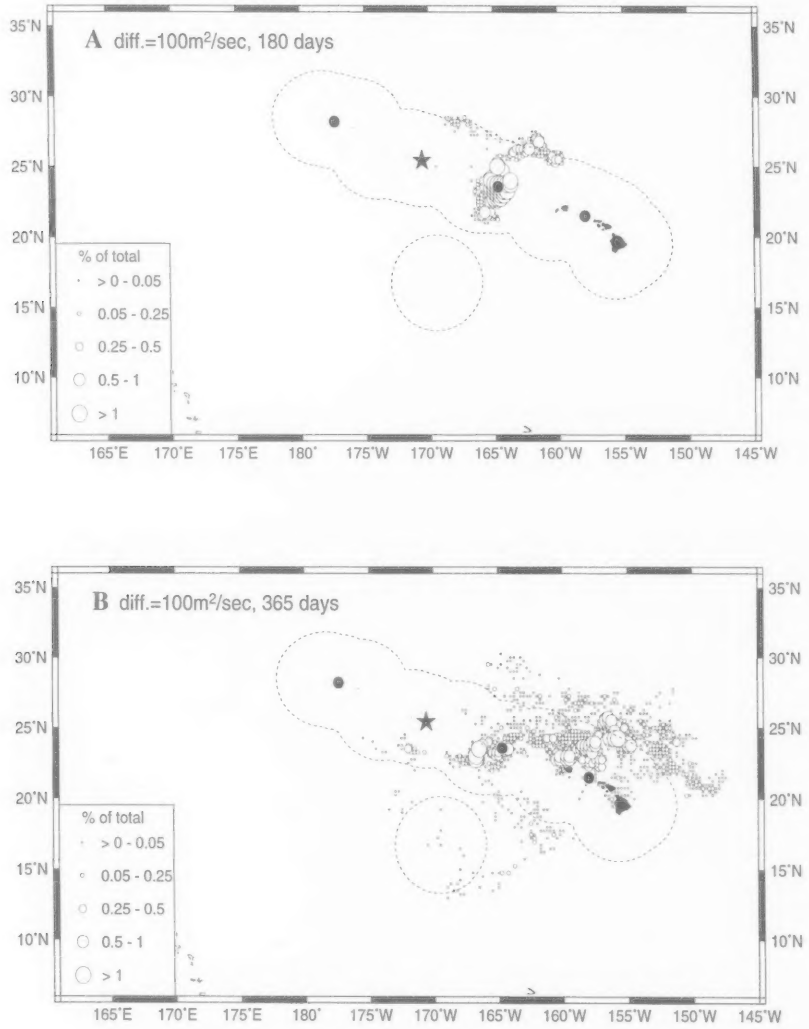

Figure 6

Simulated spatial distribution of 5000 larvae (**A**) 180 and (**B**) 360 days after release on 1 July 995 at Maro with an eddy diffusion rate of 100 m^2/sec. Solid circles denote Oahu, Necker, and Midway Islands, and the star marks Maro Island.

which the topography drops steeply to midocean depths. For Necker, Maro, and Oahu, the radius of the 200-m isobath is about 70 km. Oceanographic features resulting from interactions with topography that larvae might detect will certainly extend some distance beyond the 200-m isobath, perhaps a distance equal to the radius of the bank. Thus, as an index of larval recruitment to a bank, we assumed that larvae that were within 140 km of a bank 365 days after release would recruit to that bank. The choice of 140 km was somewhat arbitrary but because we used the index as a relative and not absolute index, the results were not particularly sensitive to this distance.

Results

Simulations were performed to describe the larval spatial dynamics from 5000 larvae released from all four banks for the 4-month summer spawning season (May–August) and the 2-month winter spawning season (November and December). The results indicated that there are spatially distinct patterns that generally persist

between years and spawning seasons and that were seen, for example, in the distribution of 1-year-old larvae in July 1995 (Fig. 7). Larvae released from Midway were advected eastward, larvae from Maro were advected east and south, larvae from Necker were advected east and south, and larvae from Oahu were advected primarily southwest (Fig. 7). A fairly persistent meander at about 26°N concentrated larvae zonally, whereas persistent westward flow at the southern end of the archipelago advected Oahu larvae westward (Fig. 7). At the center of the archipelago, specifically at Maro and Necker, a substantial portion of larvae remained close to the bank where they were spawned, even after 12 months, whereas at the ends of the archipelago, at Midway and Oahu, advection was high (Fig. 7). Further, although Necker receives abundant larvae spawned at Maro, relatively few larvae from Necker reached Maro (Fig. 7). The results, averaged over three years, showed that the percentage of larvae released at a bank and that were within 140 km of that bank 365 days later varied considerably by bank (Table 1). Differences in this percentage between winter and summer spawning seasons were not generally large but the interannual range of this percentage often varied more than threefold (Table 1). Averaged over all three years and over the two spawning seasons, the percent of larvae within 140 km of a bank 365 days after being released at that bank was 5.5%, 9.6%, 16.7%, and 16.6% for Midway, Maro, Necker, and Oahu, respectively (Table 1).

From the three years of simulations, no radical changes from the bank-specific larval distribution patterns shown in Figure 7 were seen, only spatial extensions or contractions. For example, the distribution of larvae 365 days after spawning at Necker had a northeast and southwest orientation, and larvae spawned in 1993 at Necker Island were advected east and southwest to a greater extent than larvae in 1994 or 1995 (Fig. 8).

Table 1

Mean percentage of larvae that were within 140 km of their bank of origin 365 days after release, 1993–96.

Release season	Bank	Mean percent (interannual range)
Summer	Midway	3.1 (1.8–4.7)
	Maro	10.4 (3.9–20.4)
	Necker	15.7 (9.5–20.3)
	Oahu	11.7 (8.4–15.9)
Winter	Midway	7.9 (3.7–15.0)
	Maro	8.8 (4.9–13.8)
	Necker	18.0 (8.9–29.4)
	Oahu	21.4 (12.1–33.3)

To examine the exchange of larvae between banks, the recruitment index was calculated on the basis of the bank at which the larvae originated, for both summer and winter spawning seasons, with 5000 larvae released from each bank (Table 2). The results were similar for both spawning seasons. Recruitment to Midway came almost entirely from larvae spawned at Midway. Recruitment to Maro was based largely on larvae from Maro and Midway; only 10–21% of the recruits at Maro came from Necker and Oahu. Necker had the broadest geographic source of recruits, receiving substantial larvae from all four banks. Oahu's recruits come from Maro, Necker, and Oahu (Table 2).

Discussion

The altimetry data from T-P provide a new tool to investigate recruitment questions. However, this approach has several limitations. First, because the geoid is not known, an estimate of mean dynamic topography (Levitus) was added to the T-P sea surface height anomalies. Although the accuracy of the

Table 2

Mean percentage of 12-month larvae within 140 km of each bank by bank of origin, 1993–96.

Release season	Destination bank	Bank of origin			
		Midway	Maro	Necker	Oahu
Summer	Midway	100	0	0	0
	Maro	59	31	9	1
	Necker	5	47	32	16
	Oahu	0	28	41	31
Winter	Midway	91	7	2	0
	Maro	49	30	18	3
	Necker	10	29	37	24
	Oahu	0	19	31	50

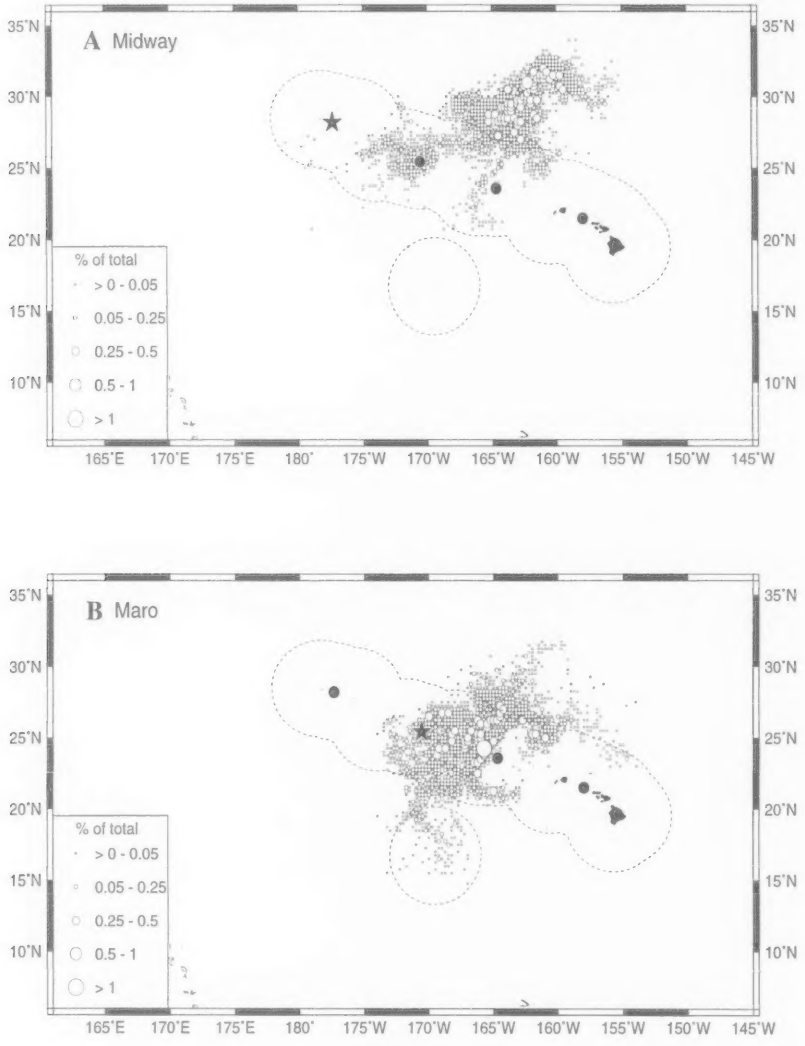

Figure 7

Simulated spatial distribution of 5000 larvae 365 days after release on 1 July 1994 at (**A**) Midway, (**B**) Maro, (**C**) Necker, and (**D**) Oahu, with an eddy diffusion rate of 500 m^2/sec. The star denotes the bank from which larvae were released. Solid circles mark the other three banks.

Levitus mean varied depending on the spatial and temporal distribution of the underlying data, it was likely that there were biases that may have had an impact on the accuracy of the estimates of absolute geostrophic current. A second limitation is that the spacing between data tracks, especially in mid- and low-latitude regions, may have been too broad to completely resolve many important finescale and mesoscale physical features. Further, this tool is appropriate only in situations where geostrophic transport is the most significant source of larval transport, situations, for example, where larvae are below the shallow Ekman layer.

In our application, this approach leads to a new hypothesis on the spatial dynamics of lobster larval recruitment in the Hawaiian Archipelago. From the simulations, we found that position of a spawning bank within the archipelago influences both the number of larvae spawned at a bank that will recruit to that bank as well as the recruitment that a bank will receive from other banks. Specifically, the results indicated that larvae are transported down the ridge from the north-

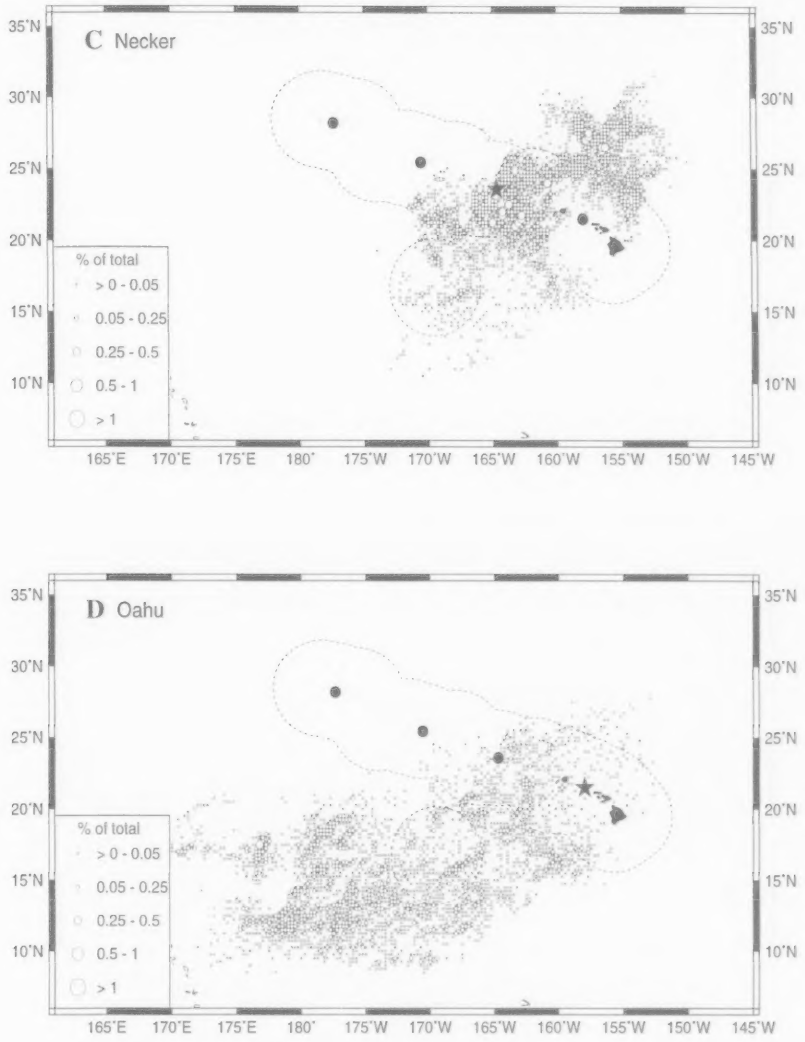

Figure 7 (continued)

west to the southeast to Necker and then southwest. Necker's persistent spiny lobster population and fishery appear to be the result of its location where it both receives larvae from banks to the northwest and southeast and also has a high retention of its own larvae. Only 670 km to the northwest, Maro's retention rate was only about one-half that of Necker, and although it contributed larvae to Necker, it did not receive any substantial contribution of larvae from Necker. This finding explains why recruitment at Maro remained depressed once the spawning biomass at Maro and other banks to the northwest were depleted, even though there was a substantial spawning biomass at Necker. However, it raises questions. Why were Maro and other northern banks so productive during the 1980s? Was the transport regime in the 1980s different, so that Maro and northern banks lost fewer larvae to the southeast and perhaps even received considerable larvae from Necker? Alternatively, because the fishery began only in the late 1970s, was recruitment always so weak at Maro and at other northern banks that the collapse at the end of the 1980s represented simply a response to overfishing an unexploited population? Although we cannot answer these questions, the results suggest that if the transport regime observed during 1993–96 persists, increased recruitment to Maro and other banks to the northwest may require an increase in the spawning population at Maro and other northern banks. Research on a similar species of spiny lobster, *P. argus*, in the Bahamas found physical trans-

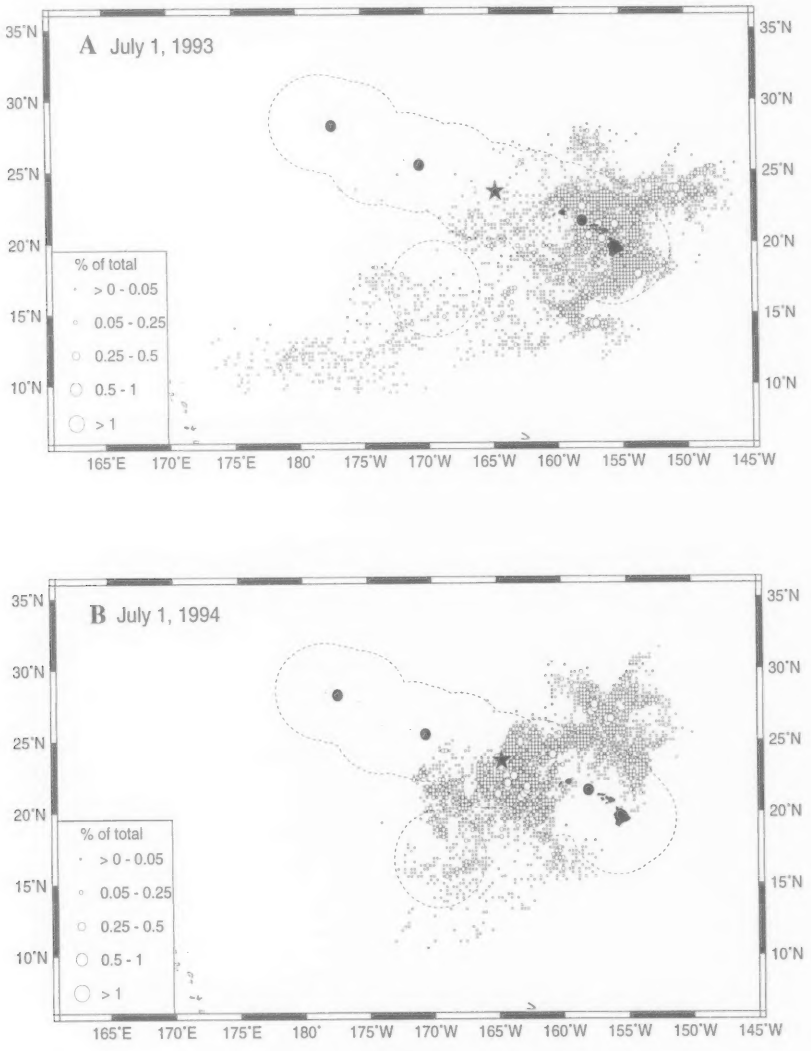

Figure 8

Simulated spatial distribution of 5000 larvae 365 days after release at Necker on (**A**) 1 July 1993, (**B**) 1 July 1994, and (**C**) 1 July 1995, with an eddy diffusion rate of 500 m^2/sec. Solid circles denote Oahu, Maro, and Midway Islands, and the star marks Necker Island.

port important to the spatial distribution of larvae (Lipcius et al., in press).

However, it is important to remember that larval abundance is necessary but not always sufficient for good recruitment and that other factors, such as habitat and predators, may also be important. Further, work to improve the input parameters and to validate these simulation results is certainly needed. For example, the results are certainly sensitive to the larval depth distribution as a function of larval age. Because these simulations produce near-real time spatial distributions, larval surveys could be designed to sample larvae in areas where the simulations show high and low larval densities in order to evaluate the model results. The model results can also be evaluated by comparing bank-specific recruitment index time series against estimated recruitment to the fishery three years later. Further, genetic studies based on DNA analyses may be more sensitive than the earlier electrophoretic studies in testing the apparent lack of mixing between regions of the archipelago suggested by these simulations. Given the hypothesis that transport was generally from

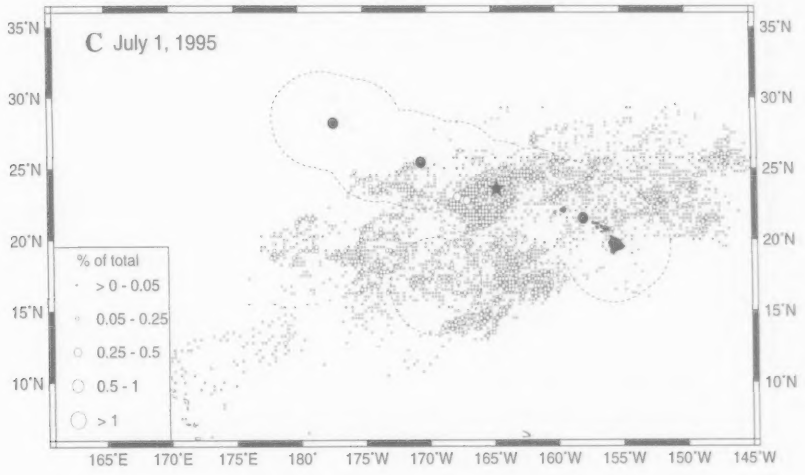

Figure 8 (continued)

Midway to Necker, this results in a testable hypothesis that genetic variance should be greater at Necker than at Midway.

Acknowledgments

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Abstract.—Monte Carlo simulation from probability distributions is often favored as a means of quantifying the uncertainty in the results of a population analysis. Observed data are combined with simulations from a population model by using subjective distributions for model parameters for which no data are available. The results from such methods can unfortunately be inaccurate unless care is taken in the combination of these simulations and the observed data. A Monte Carlo method was proposed at the 1996 meeting of the Scientific Committee of the International Whaling Commission for the assessment of the Bering-Chukchi-Beaufort Seas stock of bowhead whales. We show that this method is potentially inaccurate, and as such, it appears to be unsuited to the bowhead application and thus possibly to other similarly structured management problems.

A proposed stock assessment method and its application to bowhead whales, *Balaena mysticetus*

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The variability in parameter estimates from a population analysis is of great interest to stock assessment scientists. Monte Carlo simulation is an intuitively appealing and easily applied strategy for quantifying this uncertainty. Over the past six years, various Monte Carlo assessment methods for the Bering-Chukchi-Beaufort stock of bowhead whales, *Balaena mysticetus*, have been discussed by the Scientific Committee of the International Whaling Commission (IWC). A Bayesian approach (Raftery et al., 1995) was adopted and used as the basis for the IWC assessment of the stock in 1994. The method was developed after a 1991 Scientific Committee (SC) recommendation that methods for taking full account of uncertainty about inputs and outputs to population dynamics models be developed. An alternative maximum likelihood approach was also used for bowheads (Butterworth and Punt, 1995; Punt and Butterworth, 1996). In contrast to the adopted method, the latter approach does not allow for uncertainty in the values of various biological parameters. Rather, it assumes that they are known exactly.

At the 1996 SC meeting, a modified maximum likelihood assessment to account for uncertainty in biological parameters was considered (Punt and Butterworth, 1997). The assessment method was an application of a Monte Carlo approach developed by Restrepo et al. (1991, 1992). Punt and Butterworth (1997) cited an example of the use of the Monte Carlo approach by the International Commission for the Conservation of Atlantic Tunas, and Restrepo et al. (1992) applied their approach to swordfish and cod fishery assessments.

In our paper, we review the proposed Monte Carlo approach, both in general and in the specific bowhead application, and evaluate its performance and its compliance with established statistical principles. We show that in some circumstances the method can provide suboptimal results for bowhead as-

sessment, and it may thus be unsuitable for more general fisheries management problems. In order to illustrate the potential pitfalls of the method, some simulations were performed. The paper is presented solely as a scientific appraisal of the suggested approach, and the examples given are purely illustrative. We show how modifications of the technique can lead to improved performance, but we do not formally propose any alternative assessment methods here.

The Monte Carlo approach

Description

Restrepo et al. (1992) described an approach to quantifying the uncertainty in the results of sequential population analyses for various fish stocks. They motivated their approach by noting that

> Fisheries managers recognize the dangers of accepting parameter estimates without consideration of the variability inherent in the estimates of fish stock status and related parameters... If all sources of error are not appropriately accounted for, then estimates of the uncertainty in the assessment results may be too small.

This Monte Carlo approach (hereafter MCA) proceeds as follows. Probability distributions are used to describe uncertainty in the inputs to an assessment model. These distributions are constructed in two ways:

1 If observed data are available for a specific input, a parametric statistical model for the data is assumed, and the parameters are estimated by maximum likelihood. A parametric bootstrap is then used to obtain a sample of input values. These values are used as values of the input in the assessment model.
2 If no data relevant to the input are available, a subjective "prior" distribution, representing educated guesses about the true value, is placed upon it.[1] A sample from this prior is used in the assessment model.

The second case occurs in many stock assessment procedures. For instance, a prior was needed for natural mortality, M, in the swordfish assessment of Restrepo et al. (1992). Similarly, we required a subjective distribution for the growth rate parameter, MSYR in the bowhead whale example in the section "Application of MCA to bowhead whale assessment."

[1] Such a distribution is effectively a Bayesian prior distribution. However, since the framework of MCA is not Bayesian, Restrepo et al. (1992) do not refer to such a distribution as a prior.

The next step in MCA is to compare simulated model outputs, such as a time trajectory of stock sizes to observed data, in order to formulate a likelihood (assuming lognormal deviations). Many input parameter sets are drawn randomly from the specified input distributions (i.e. either from data-based bootstrap or subjective prior), and for each set, a conditional maximum likelihood estimate (MLE) is calculated for quantities of interest, given the fixed input parameters and the observed data. The simulation distribution of such conditional MLEs is used to quantify uncertainty. The simulation is viewed as translating input uncertainties into output uncertainties.[2]

MCA is suggested for situations where (possibly many) nuisance parameters exist. These are typically the model input parameters for which no informative data are available. The basic strategy is to estimate the quantities of interest (e.g. current stock size and production rate) conditional on values of the nuisance parameters and then to integrate over the prior for the nuisance parameters. The distribution of the conditional estimates of the parameters of interest is then examined for the purposes of inference. For example, if $\hat{\theta}_\gamma$ is an estimator of θ, conditional on nuisance parameters γ, then

$$\hat{\theta}_{(1)} = \int \hat{\theta}_\gamma p(\gamma) d\gamma \qquad (1)$$

is an MCA estimate of θ, where $p(\gamma)$ is the prior for γ.[3]

In practice, the integral in Equation 1 is not calculated exactly; it is approximated by using the Monte Carlo simulation described above. In the form of an algorithm, MCA proceeds as follows:

1 Obtain the MLE $\hat{\theta}_{\gamma_0}$ from the observed data $\boldsymbol{X}$ and a likely value γ_0.
2 Sample γ^* from the prior $p(\gamma)$.
3 Sample pseudo-data $\boldsymbol{X}^*$ from a distribution with density $f(\boldsymbol{x}; \tilde{\psi}(\boldsymbol{X}))$, where $f(\boldsymbol{x}; \psi)$ is a model for the data but not necessarily the assessment model and where $\tilde{\psi}(\boldsymbol{X})$ is an estimate of the parameters of this model. $\tilde{\psi}(\boldsymbol{X})$ may depend on the results of step 1, namely $\hat{\theta}_{\gamma_0}$ and γ_0, or even on standard MLEs $\hat{\theta}$ and $\hat{\gamma}$. An example of f would be to assume $\boldsymbol{X}^* \sim N(\boldsymbol{X}, \hat{\psi})$, where $\hat{\psi}$ is an estimated dispersion matrix.

[2] Restrepo et al. (1992) also consider uncertainty in the assessment model itself, but this issue is not of primary interest here. In the bowhead whale application, the assessment model is fixed by the IWC.

[3] In general these parameters may be multivariate vectors. For simplicity, we restrict our focus to scalar parameters in the subsequent examples.

4 Find the conditional MLE $\hat{\theta}_{\gamma^*}$ given γ^* by using the simulated data $\boldsymbol{X}^*$. Store this value.
5 Repeat steps 2–4 many times to obtain a collection of $\hat{\theta}_{\gamma^*}$'s.

MCA inference about θ is then based on the distribution of this collection of $\hat{\theta}_{\gamma^*}$'s. Typically, the original $\hat{\theta}_{\gamma_0}$, or the mean or median of the Monte Carlo sample, is used as a point estimate, and the 0.025 and 0.975 quantiles form the bounds of a 95% confidence interval.

The Monte Carlo approach is not a straightforward extension of a sensitivity analysis. Usually, in a sensitivity analysis, a small number of alternative parameter values are tried, and the individual point estimates and confidence intervals obtained by using each parameter set are tabled. Inference usually follows from a single analysis where a particular baseline parameter has been set; the remainder of the table is used to assess how conclusions would change under different modeling assumptions. With MCA, a potentially vast number of parameter values are tried, and an overall confidence interval is obtained by pooling the results of each individual analysis, effectively integrating over the distribution of the nuisance parameters. We show in the rest of this paper that this integration is a source of potential bias.

The MCA technique is potentially highly sensitive to violations of its assumptions. If one is going to express uncertainty in the value of a parameter by means of a probability distribution, then this distribution should be treated as a prior in a fully Bayesian setup. The method given in Equation 1 provides estimators that will not necessarily possess the desirable properties of either Bayesian or ML estimators. A general overview of Bayesian methods is given by Lee (1997).

In a Bayesian framework, the best estimator of θ (with respect to squared error loss) is the posterior mean $E(\theta|\text{data})$, therefore it would be better to define the estimator as

$$\hat{\theta}_{(2)} = E(\theta|\text{data}) = E\big[E(\theta|\gamma,\text{data})\big] = \int \hat{\theta}_\gamma \pi(\gamma|\text{data}) d\gamma, \quad (2)$$

where $\hat{\theta}_\gamma$ = the posterior mean of θ conditional on γ, and
$\pi(\gamma|\text{data})$ = the posterior distribution of γ.

One might regard Equation 2 as a general strategy and use it in cases where $\hat{\theta}_\gamma$ is not necessarily the Bayesian estimator. In this case, however, the properties of $\hat{\theta}_{(2)}$ are not clear.

A simple point estimation example

Schweder and Hjort[4] first identified potential weaknesses with MCA, and they described two situations where differences between the methods of Equations 1 and 2 arose. The first of these is repeated here: consider a random sample of size n from a normal distribution with mean μ and variance σ^2, denoted $X_i \sim N(\mu, \sigma^2)$ for $i = 1, \ldots, n$. Assume that there is a $N(\mu_0, \tau_0^2)$ prior for μ, where μ_0 and τ_0^2 are the prior mean and variance respectively. Let σ^2 be the parameter for which inference is desired. μ is a nuisance parameter and σ^2 is regarded as fixed. The maximum likelihood estimate of σ^2 conditional on μ is

$$\hat{\sigma}^2_\mu = \frac{1}{n}\sum_{i=1}^{n}(x_i - \mu)^2.$$

The estimators given by Equations 1 and 2 are then

$$\hat{\sigma}^2_{(1)} = E_{prior}(\hat{\sigma}^2_\mu) = \frac{1}{n}\sum_{i=1}^{n}(x_i - \mu_0)^2 + \tau_0^2$$

and

$$\hat{\sigma}^2_{(2)} = E_{posterior}(\hat{\sigma}^2_\mu) = \frac{1}{n}\sum_{i=1}^{n}(x_i - \mu_{post})^2 + \tau^2_{post}$$

respectively, where μ_{post} and τ^2_{post} are the posterior mean and variance of the nuisance parameter μ. For this simple case, we have closed form expressions for Equations 1 and 2, and no Monte Carlo sample from the prior for μ is required. Note that in Equation 2, $\hat{\sigma}^2_\mu$ (the conditional maximum likelihood estimator of σ^2) is used as $\hat{\theta}_\gamma$. In addition we note that $\hat{\sigma}^2_{(2)}$ depends on σ^2 because both μ_{post} and τ^2_{post} are functions of σ^2. In other words, the estimator $\hat{\sigma}^2_{(2)}$ depends on the quantity it is trying to estimate. This occurs when $\hat{\theta}_\gamma$ is not the Bayesian posterior mean of θ conditional on γ. In our examples, we simply plugged in the ordinary MLE where needed to remove this dependency. Thus, to evaluate $\hat{\sigma}^2_{(2)}$ here, $\hat{\sigma}^2_{std}$ was used as a plug-in estimate of σ^2 in the expressions for μ_{post} and τ^2_{post}. $\hat{\sigma}^2_{std}$ is the usual MLE of σ^2 and is what would normally be used if conditioning on μ were not of interest.

We know from standard theory that $\hat{\sigma}^2_{std} \to \sigma^2$ as $n \to \infty$. Because $\tau^2_{post} \to 0$ and $\mu_{post} \to \mu$, we have that $\hat{\sigma}^2_{(2)} \to \sigma^2$ as $n \to \infty$. $\hat{\sigma}^2_{(1)}$, on the other hand, will converge to σ^2 only if $\mu_0 = \mu$ and $\tau_0^2 = 0$. It follows that $\hat{\sigma}^2_{(1)}$ will, in general, yield accurate estimates only if

[4] Schweder, T., and N. L. Hjort. 1997. Indirect and direct likelihoods and their synthesis—with an appendix on minke whale dynamics. Paper SC/49/AS9 presented to the IWC Scientific Committee, October 1997.

μ_0 is close to μ and τ_0^2 is small. We show later the practical implications of choosing an estimator for which the data either do ($\hat{\sigma}^2_{(2)}$) or do not ($\hat{\sigma}^2_{(1)}$) eventually dominate the prior.

An alternative approach that does not involve conditioning on μ is a fully Bayesian analysis where both μ and σ^2 are random variables. This approach requires the specification of a joint prior on μ and σ^2. One such prior is the indifference or "reference" prior (Jeffreys, 1961)

$$p(\mu,\sigma^2) \propto \frac{1}{\sigma^2}.$$

The resulting marginal posterior mean of σ^2 is the best Bayesian estimator of this parameter and is given by

$$\hat{\sigma}^2_{(3)} = \frac{1}{n-3}\sum_{i=1}^{n}(x_i - \bar{x})^2.$$

To investigate the difference between the MCA estimate in Equation 1 and the ad hoc "Bayes" approach in Equation 2, we performed some simple simulations. For each of nine combinations of μ_0 and τ_0^2, a random sample of size n = 1000 was drawn from a $N(\mu$=50, σ^2=100) distribution. In each case, $\hat{\sigma}^2_{(1)}$, $\hat{\sigma}^2_{(2)}$, $\hat{\sigma}^2_{(3)}$, and $\hat{\sigma}^2_{std}$ were determined. The results are shown in Table 1.

The results show very poor performance for $\hat{\sigma}^2_{(1)}$, and good, similar performances for $\hat{\sigma}^2_{(2)}$, $\hat{\sigma}^2_{(3)}$, and $\hat{\sigma}^2_{std}$. In this simple case, the analyst would presumably never choose MCA or the ad hoc "Bayes" method over optimal estimators, such as $\hat{\sigma}^2_{(3)}$ and $\hat{\sigma}^2_{std}$. The key point of this example is that if conditioning on nuisance parameters is to be used, the strategy presented in Equation 2 appears to be preferable to the MCA estimate in Equation 1. As mentioned earlier, the use of Equation 2 has a severe limitation of its own; we therefore do not regard it as a viable alternative approach.

There is considerable literature on the role of conditioning in inference. Reid (1995) has presented a review of recent developments.

Table 1

Simulation results for the example of Schweder and Hjort (See Footnote 4 in the main text).

			Estimators of σ^2 (true value is 100)		
μ_0	τ_0^2	MCA: $\hat{\sigma}^2_{(1)}$	Ad hoc "Bayes": $\hat{\sigma}^2_{(2)}$	Full Bayes: $\hat{\sigma}^2_{(3)}$	Std. MLE: $\hat{\sigma}^2_{std}$
50	1	95.4	94.5	94.7	94.4
	9	102.0	93.0	93.2	92.9
	25	121.0	95.9	96.1	95.8
60	1	198.4	100.4	99.8	99.5
	9	197.2	92.1	92.3	92.0
	25	220.8	99.9	100.1	99.8
70	1	499.8	106.6	103.4	103.1
	9	490.0	106.4	106.5	106.2
	25	530.4	109.7	110.0	109.6

Confidence interval estimation

The example in the section "A simple point estimation example" illustrates poor performance for MCA with regards to point estimation. Similar problems occur when constructing confidence intervals.

Consider the following example: let $X_i \sim U(\gamma-\theta\gamma, \gamma+\theta\gamma)$ for $i = 1,\ldots,100$, denote a random sample from a uniform distribution with bounds specified by the given functions of θ and γ. Let γ be the nuisance parameter. The unconditional MLEs are $\hat{\gamma} = (\max X_i + \min X_i)/2$ and $\hat{\theta} = (\max X_i - \min X_i)/(\max X_i + \min X_i)$. The conditional MLE of θ given γ is $\hat{\theta}_\gamma = (\max X_i - \min X_i)/(2\gamma)$.

Suppose the nuisance parameter, γ, has a $U(a,b)$ prior, $0 \le a < b$. MCA would proceed as follows:

1 Sample $\gamma^* \sim U(a,b)$.
2 Use the parametric bootstrap (e.g. Efron and Gong, 1983) to sample $X_i^* \sim U(\hat{\gamma}-\hat{\theta}\hat{\gamma}, \hat{\gamma}+\hat{\theta}\hat{\gamma}), i = 1, \ldots, 100$.
3 Find the conditional MLE, $\hat{\theta}_{\gamma^*}$, using the bootstrap data, and conditioning on the current γ^*.
4 Store $\hat{\theta}_{\gamma^*}$ and go to step 1. Use the collection of $\hat{\theta}_{\gamma^*}$'s to obtain a confidence interval with the quantile method.

The ad hoc "Bayes" method, which relies on sampling from the posterior, proceeds with the same steps except that step 1 is replaced by

1. Sample γ^* from its posterior distribution.

Here, if we think of the likelihood as a function of γ only, then the posterior for γ is proportional to

$$\prod_i \left[\frac{1}{2\theta\gamma} I(\gamma-\theta\gamma \le X_i \le \gamma+\theta\gamma)\right] I(a \le \gamma \le b),$$

where I is an indicator function given by

$$I(x) = \begin{cases} 1 \text{ if } x \text{ is True} \\ 0 \text{ if } x \text{ is False.} \end{cases}$$

Because this posterior depends on θ, we plugged in $\hat{\theta}$ in the same way as we did for the ad hoc "Bayes" method in the section "A simple point estimation example."

In a simulation example, we let $\theta = 4$, $\gamma = 4$, $a = 0$, and $b = 8$, so that the true value for γ was at the midpoint of its prior. The MLEs were $\hat{\theta} = 4.06$ and $\hat{\gamma} = 3.88$. The 95% MCA interval for θ was (1.99, 87.55). The interval obtained with the ad hoc "Bayes" method was (3.78, 4.03). The MCA interval was 342 times wider than the second interval, and 2.7 times wider than the range of the observed data.

Note that the MLE $\hat{\theta}$ is not contained in the second interval above. This is an undesirable result of the ad hoc "Bayes" method here. One possible remedy is as follows: instead of simply plugging $\hat{\theta}$ into the posterior for γ each time we sample from it, we could attempt to "integrate over theta" by plugging in a different estimate of θ on each occasion. Each of these plug-in values for θ can be obtained by calculating the MLE of θ from a nonparametric bootstrap sample of the real data X. The confidence interval resulting from this strategy was (3.59, 4.08), so the MLE is now contained in the interval. We stress that this is again an ad hoc solution and we strongly favor standard maximum likelihood or Bayesian methods over either MCA or the ad hoc "Bayes" method.

Finally, the example can also be twisted so that the MCA interval is too narrow. Suppose $X_i \sim U(\gamma - \theta\gamma^2, \gamma + \theta\gamma^2)$. This leads to $\hat{\theta}_\gamma = (\max X_i - \min X_i)/(2\gamma^2)$, a cusp-shaped function of γ over any interval that includes 0. Thus, considering γ priors of the form $U(-a,a)$ for $a > 0$, we observed that MCA leads to the surprising result that the width of a quantile-based confidence interval for θ approaches 0 as a increases, while holding the observed data fixed. In other words, the width of the confidence interval is entirely dependent on the prior, and wider priors lead to narrower MCA confidence intervals.

Application of MCA to bowhead whale assessment

Punt and Butterworth (1997) examined the applicability of MCA in the assessment of the Bering-Chukchi-Beaufort stock of bowhead whales. As with the swordfish assessment of Restrepo et al. (1992), the approach involved generation of pseudodata with a parametric bootstrap. In the bowhead case, the real data consisted of abundance estimates and corresponding CV estimates for several years, and observed age-class proportions. Thus, each MCA simulation consisted of the following:

1 *Bootstrapping of data*. A series of pseudo-abundance estimates is bootstrapped from the observed data (Table 1 in Punt and Butterworth, 1997). Each estimate is assumed to be independent and from a lognormal distribution with mean and CV equal to the observed estimates from that year. Pseudodata for fractions of calves and matures are generated from Table 4 of IWC (1995).
2 *Sampling of biological nuisance parameters from priors*. Parameters such as age at maturity and natural mortality rates are generated from prior distributions from IWC (1995).
3 *Conditional estimation*. Conditional on the values of the nuisance parameters, maximum likelihood estimation is used with an age-structured density dependent population dynamics model to obtain estimates of the parameters of interest: carrying capacity (K) and a productivity parameter (MSYR). The likelihood contains contributions from both the abundance and proportion data.
4 *Uncertainty estimation*. The variation in conditional MLEs is used to represent uncertainty.

Note that K and MSYR are the parameters of interest (denoted by θ in our previous notation), whereas the other biological parameters take the role of γ. The distributions from which they were simulated are the prior distributions. The results of 1000 replications of this procedure are used to form confidence intervals.

A simple population dynamics model

For the purposes of illustration, we applied MCA to a simple population dynamics model (PDM). This is a non-age-structured density dependent PDM given by

$$P_{t+1} = P_t - C_t + 1.5(MSYR)P_t\left(1-(P_t / K)^2\right), \quad (3)$$

where P_t = the population in year t, with $t = 0$ corresponding to the baseline year before commercial hunting started (here 1848);
K (or P_0) = the initial population size or carrying capacity;
MSYR = the maximum sustainable yield rate of production as a proportion of the population aged 1+; and
C_t = the number of whales killed by hunting in year t (known exactly).

This model is much simpler than the BALEEN II PDM (de la Mare and Cooke[5]) used by the IWC for

[5] de la Mare, W. K., and J. G. Cooke. 1993. "BALEEN II: The population model used in the Hitter-Fitter Programs". Unpublished manuscript available from the IWC Secretariat, The Red House, 135 Station Road, Histon, Cambridge, UK CB4 4NP.

bowhead assessment, but it nevertheless captures many of the essential features of the bowhead population. The model is viewed as having two inputs (K and MSYR) and one output (P_{1993}); with fixed values of MSYR and the initial K, Equation 3 is applied recursively until P_{1993} is obtained. We use the term "model input" for input parameters whose true value is uncertain. Since the time series of catches C_t is exactly known, we regard it as a set of constants in Equation 3, rather than as a set of model inputs.

In our simplified version of the bowhead analysis, we treated MSYR as a nuisance parameter (γ in our previous notation) and K was the parameter of interest (the θ from before). The only parameter about which we observed data for a parametric bootstrap was P_{1993}. MSYR was assigned a subjective prior distribution. In terms of implementation, we ran the model "backwards" with P_{1993} and MSYR as inputs and K as output. A Newton-Raphson algorithm was used to solve for K. As a result, we effectively had P_{1993} and MSYR as model inputs, and K (obtained conditionally on MSYR and the data) as the model output.

Implementation of MCA and a Bayesian approach

To evaluate MCA, we examined its performance when the true whale stock status was known. "True" values of K and MSYR were selected, and the PDM was run to obtain the "true" value of P_{1993}. Because K (the parameter of interest here) has a "true" value, we were able to assess the accuracy of the estimates produced by the simulations.

MCA was applied to the simple PDM of Equation 3 in a number of steps. The prior for the nuisance parameter MSYR was gamma(8.2, 372.7), and the likelihood for the observed total population in 1993 was $N(P_{1993},626^2)$. These choices were based on IWC consensus (IWC, 1995) and were the same as used in previous work (Raftery et al.[6]).

We assumed that we had a single observation from the likelihood for P_{1993}. In practice such an observation is usually obtained by means of a census. The observation is typically a maximum likelihood estimate of P_{1993}, therefore we denoted it by $\hat{P}_{1993}$.

An original conditional MLE was obtained by conditioning on a "likely" point estimate of MSYR, say $MSYR_0$. We chose $MSYR_0 = 0.02$, the mean of the prior for MSYR. The model was then run backwards (i.e. with $\hat{P}_{1993}$ and $MSYR_0$ as inputs) and the likelihood maximized. The resulting output was the conditional maximum likelihood estimate $\hat{K}_{MSYR_0}$ of K because (given $MSYR_0$) it lead to the value of P_{1993} that maximizes the likelihood.

The MCA estimation then proceeds as follows:

1 Draw $\hat{P}^*_{1993}$ from $N(\hat{P}_{1993},626^2)$. This is the parametric bootstrap from a distribution with mean given by the observed total population in 1993.
2 Draw $MSYR^*$ from the prior for MSYR.
3 Obtain $\hat{K}_{MSYR^*}$ by running the model backwards with $\hat{P}^*_{1993}$ and $MSYR^*$ as inputs.
4 Repeat steps 1–3 many times to form a collection of $\hat{K}_{MSYR^*}$ estimates. Like Punt and Butterworth (1997), we used 1000 replications.
5 Use $\hat{K}_{MSYR_0}$ and the distribution of the $\hat{K}_{MSYR^*}$ estimates to obtain inference about K. Specifically, the distribution of the $\hat{K}_{MSYR^*}$ estimates shows how the conditional MLE of K changes as MSYR is varied according to its prior.

For comparison with MCA, consider a fully Bayesian analysis which involves specifying priors for every model parameter, i.e. K, MSYR, and P_{1993}. This introduces an extra complication in that the input distributions and the model together induce a distribution on the output. There are thus two distributions (the specified prior and the induced distribution) on the output that need to be combined or reconciled in some manner. For our "backwards" implementation of the model here, the priors for MSYR and P_{1993} induce a prior on the output K. This issue has received considerable attention at the IWC and work in the area is ongoing. A possible solution involving logarithmic pooling of the two distributions is discussed in Raftery et al.[6] and Raftery and Poole.[7]

For this example, it was useful to compare a Bayesian approach with MCA, but avoiding the added complexity of the prior incoherence. This could be achieved if we simplified the Bayesian analysis slightly by ignoring the prior on the output K. We had a prior for MSYR and a likelihood for P_{1993} as we did in the MCA implementation above. In addition, we now also had a $N(7800,1300^2)$ prior for P_{1993}. This was the prior used in Raftery et al.[6] and was again based on IWC consensus. The prior and likelihood were combined to yield a posterior distribution for P_{1993}. Because we had no data on MSYR, its prior was not updated to a posterior. The only operational difference between MCA and the Bayesian method was in the generation of values for P_{1993}: with MCA,

[6] Raftery, A. E., D. Poole, and G. H. Givens. 1996. The Bayesian synthesis assessment method: resolving the Borel Paradox and comparing the backwards and forwards variants. Paper SC/48/AS16 presented to the IWC Scientific Committee, June 1996.

[7] Raftery, A. E., and D. Poole. 1997. Bayesian synthesis methodology for bowhead whales. Paper SC/49/AS5 presented to the IWC Scientific Committee, October 1997.

values were bootstrapped from a distribution whose parameters were determined by maximum likelihood; with Bayes, they were sampled from the posterior.

Simulation results

Simulations were performed by using three sets of "true" parameters as shown in the first three columns of Table 2. The values of MSYR in these three sets of simulations correspond to the 0.5, 0.975, and 0.025 quantiles (respectively) of the gamma (8.2, 372.7) prior for this parameter. In this way, we investigated the performance of the method when the true MSYR is at the center and the boundaries of its prior 95% probability interval. In each case, a value of K was chosen such that extinction did not occur and P_{1993} was positive.

The first set of simulations represents a scenario where the mean of the prior for MSYR happens to coincide with the true value. If we use the prior mean as a point estimate (or "best guess") of MSYR, then our point estimate and the true value are the same. For this set, then, we would expect all assessment methods to provide accurate inference about K. The remaining two sets of simulations represent scenarios where our prior is inaccurate, i.e. the true MSYR is either larger or smaller than the prior mean (which remains unchanged). In these cases, this inaccuracy is naturally going to cause the resulting distribution of the output K to be biased. All assessment approaches will be affected by this bias, particularly with respect to their point estimates of K. Indeed, these parameter sets represent situations that all assessment scientists would like to avoid. The key point of interest is the extent to which a method can be insensitive to poor prior information and still provide somewhat reliable inference.

The results of the simulations are shown in Table 2. For each of the three sets of true parameters, the MCA analysis was run three times by using the 0.025, 0.5, and 0.975 quantiles of the normal likelihood as the observed 1993 population, $\hat{P}_{1993}$. Then, this entire simulation design was replicated 500 times. The quantiles shown are MCA medians for $\hat{K}_{MSYR^*}$ across the 500 replicates, and the coverage rates (last two columns) show the percentage of the 500 replicates for which the estimated 95% MCA or Bayes confidence interval covered the truth.

In the first set of simulations, where the true MSYR and the prior mean MSYR_0 were exactly equal, the conditional MLE $\hat{K}_{MSYR_0}$ was very accurate. This is to be expected in this optimistic (if somewhat unlikely) scenario. The MCA confidence intervals provided by $\hat{K}_{MSYR^*}$ covered the true K in all cases, as did the confidence intervals obtained with the Bayesian method. Also, the estimation was fairly insensitive to the accuracy of the estimate $\hat{P}_{1993}$. A difference of 1227 whales in the estimate of P_{1993} (i.e. two standard deviations) resulted in $\hat{K}_{MSYR_0}$ changing by less than 100 whales.

In the second set, the true value of MSYR was greater than the prior mean. This resulted in K having been overestimated. Here, both MCA and Bayesian results were biased by the use of the same bad prior, but the MCA coverage was worse. If follows that the suboptimal behavior of MCA cannot be attributed solely to the choice of prior. The 95% MCA intervals provided poor coverage of the truth, worse when $\hat{P}_{1993}$ was accurate than when it was too low. For the Bayesian method, this difference was not as great. The coverage of the Bayesian intervals was somewhat better in two cases, particularly when $\hat{P}_{1993}$ was too large.

In the final set, the true value of MSYR was at the low end of the prior interval, and we observed that K

Table 2

Simulation results for the simple bowhead whale population dynamics model (PDM).

Parameter set					MCA quantiles, $\hat{K}_{MSYR^*}$			Coverages	
MSYR	K	P_{1993}	$\hat{P}_{1993}$	$\hat{K}_{MSYR_0}$	0.025	0.5	0.975	MCA (%)	Bayesian (%)
0.02	14,700	8,733	7,506	14,640	11,230	14,360	18,870	100	100
			8,733	14,700	11,260	14,400	19,160	100	100
			9,960	14,780	11,330	14,450	19,540	100	100
0.04	11,300	9,896	8,669	14,700	11,250	14,400	19,120	68	66
			9,896	14,780	11,290	14,470	19,450	55	63
			11,123	14,880	11,580	14,560	19,840	0	23
0.01	18,500	6,971	5,744	14,570	11,270	14,300	18,430	38	54
			6,971	14,620	11,260	14,340	18,710	80	88
			8,198	14,670	11,270	14,380	19,000	99	99

was underestimated by about 4000 whales for all three values of $\hat{P}_{1993}$. The estimates of K were inaccurate regardless of the accuracy of $\hat{P}_{1993}$. Although not shown, this inaccuracy holds for the Bayesian method as well as for MCA. Both methods provided the best coverage when $\hat{P}_{1993}$ was too large, but the Bayesian method provided better coverage than MCA in the other two cases. Again, these results separated coverage problems attributable to inaccurate priors from additional performance degradation apparently introduced by opting for MCA analysis.

As a final point, these simulations and others that we ran suggest that the MCA estimates of K are heavily dependent on the prior distribution for MSYR, to the point of being undesirably insensitive to the true values of K, P_{1993}, and the data $\hat{P}_{1993}$. This behavior is more extreme than would be the case if the prior was updated to a posterior in a fully Bayesian framework. These results concur with the results in the section "A simple point estimation example," where the MCA estimates were greatly influenced by the prior mean and variance. When the prior is accurate and precise, MCA may perform well, as will Bayesian techniques. Bayesian techniques seem to weight the data more heavily in relation to the prior, than does MCA.

Relation between MCA and bootstrap

The MCA approach described in the section "Implementation of MCA and a Bayesian approach" included bootstrapping the abundance data unconditionally. A standard (conditional) bootstrap would proceed by resampling the residuals (e.g. Efron and Gong, 1983, p. 43) from the model fit. The unconditional approach used in the bowhead application introduced excess variability because bootstrapped pseudodata varied about the observed data, which in turn varied about the model fit.

The general MCA approach might be viewed as an approximation to a bootstrap that is unconditional on the model fit. In such applications (e.g. Smith and Gavaris, 1993), the interpretation of the stochasticity thereby introduced must be carefully considered if it differs from the data stochasticity that causes estimation uncertainty. When, as is permitted with MCA, the unconditional approach simulates from a subjective prior rather than from data, the method is not a bootstrap because the simulation reflects stochasticity other than that introduced by data used for estimating the parameter.

Even in the case when sufficient data are available to permit parametric bootstrap simulation of all inputs (case 1 in the section "The Monte Carlo approach"), MCA does not reduce to a parametric bootstrap of the desired estimator. A parametric bootstrap expresses sampling uncertainty about a statistic $R(\boldsymbol{X}, F(\theta))$, where $\boldsymbol{X} \sim F$, by observing the distribution of $R(\boldsymbol{X}^*, \hat{F}(\theta))$, where $\hat{F}$ is an estimate of F that depends on the data $\boldsymbol{X}$, and $\boldsymbol{X}^* \sim \hat{F}$. Variability in R is due to $\boldsymbol{X}$. A parametric bootstrap arises when a model $\hat{F}(\theta) = F(\theta)$ is fitted, or less desirably $\hat{F}(\theta) = G(\hat{\gamma})$ in some applications of MCA. In this case, $\hat{\theta}$ or $\hat{\gamma}$ should be estimated from the data, $\boldsymbol{X}$, whose stochasticity induces sampling variability in $R(\boldsymbol{X}, F(\theta))$. However, with MCA, $\hat{\theta}$ or $\hat{\gamma}$ is estimated from different data, not the data on model output parameters, although it is the uncertainty associated with estimators of output parameters that is desired. Even in this case, the sampling distributions used are effectively data-based priors, and MCA relies on the unusual approach of integrating a conditional maximization of the likelihood over the prior.

Conclusion

Theoretical investigation and simulation show that the combination of Bayesian and conditional maximum likelihood techniques used by MCA has the potential to yield quite variable or biased results, or both, though it can perform well in ideal circumstances. In some situations, a fully Bayesian or classical ML solution can be obtained by small modifications to MCA, and the optimal properties of these more standard methods are well known. For more complex problems, Bayesian and ML solutions are sometimes more difficult to obtain than is an MCA solution. However, as our examples illustrate, MCA can result in unreliable inference even in simple situations. MCA integrates a conditional maximization of the likelihood over the prior, whereas a fully Bayesian approach integrates a conditional mean. If one uses what is effectively a Bayesian prior, then it is suboptimal to use it in a non-Bayesian inference framework.

We have seen how MCA produces estimates with excessive bias. However, there may exist classes of assessment problems where, owing to some feature that is identifiable in advance, the extra bias is acceptably small. MCA could be applied to such problems because the excess bias would not cause MCA results to differ much from results produced by either fully Bayesian or ML methods. Our bowhead whale and simple examples clearly do not belong to such a class. Furthermore, in the general case, the extent to which MCA might err is not controllable or estimable by the analyst. Although MCA can produce good estimates in some applications, a method that can also go badly wrong is risky when one does not

know the extent of problems in any particular application. When priors are used, the usefulness of Bayesian approaches (when obtainable) would seem to be greater than MCA, because the effect of the priors is washed out with increasing data (contrary to what happens with MCA). When priors are not required, either Bayesian or MLE techniques might be usefully applied.

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Age and growth determination of the white shark, *Carcharodon carcharias*, from the east coast of South Africa

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Abstract.—Ages of white sharks, *Carcharodon carcharias*, from the east coast of South Africa were estimated by counting growth rings (GRs) in vertebral centra and relating them to length and mass. The vertebrae of 61 females (128–297 cm precaudal length (PCL)) and 53 males (142–373 cm PCL) were examined. Mass range was 42–442 kg for females (n=60) and 46–882 kg for males (n=53). X-radiography was used to enhance the visibility of the GRs in whole centra. Counts were made directly from the x-radiographs by one reader and from scanned x-radiographs by two readers. Count precision for each method and reader was determined by using the average percentage error (APE) index which ranged from 5.3 to 6.1%.

One shark injected with oxytetracycline (OTC) was recaptured after 942 days at liberty. The shark was tagged at 140 cm and 46 kg and grew 69 cm and 104 kg. The OTC was visible in the vertebra and there was evidence of annual growth ring deposition. This could, however, not be confirmed with centrum analyses of the entire sample.

The number of GRs counted varied in the following manner. The female and male with the lowest number of GRs, had 0 GR (131 cm PCL) and 1 GR (142 cm PCL), respectively. The female and male with the highest number of GRs, had 8 GRs (282 cm PCL) and 13 GRs (373 cm PCL), respectively. The smallest mature male had 8 GRs (293 cm PCL); there were no mature females. Von Bertalanffy parameters for the combined sexes were L_∞ = 544 cm PCL, k = 0.065/yr, t_0 = –4.4 yr. Growth calculated from predicted lengths decreased from 26 cm for sharks with 1 GR to 12 cm for sharks with 13 GRs. Gompertz parameters were w_0 = 54 kg, G = 3.94, g = 0.094/yr. Growth calculated from predicted mass increased from 23 kg (1 GR) to 94 kg (13 GRs). Back-calculated lengths and mass were lower than observed values and Lee's phenomenon was evident in both back-calculated lengths and mass but not consistently.

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The white shark, *Carcharodon carcharias*, is found worldwide in cold and temperate coastal and shelf waters (Compagno, 1984). As a large, uncommon apex predator, it has received considerable attention from scientists over the past few years. Because of its great resale value, compared with most other sharks, catches of white sharks have increased in various parts of the world, mainly in Australia and South Africa (Compagno, 1990, 1991). Claims of a declining population size in South Australian waters (Compagno, 1991; Bruce, 1992) influenced an initiative to implement protective legislation for this species in South Africa. In 1991 the South African government prohibited the catching or killing of white shark without a permit (Compagno, 1991). This measure was a preemptive protection and is to be reviewed as results of more research into the biology of this species become available (Compagno, 1991). Protection has now also been introduced in California, Florida, and Tasmania (Fergusson et al., in press), as well as in Queensland, New South Wales, South Australia, and Western Australia (Stevens[1])

Legislation in South Africa has prevented this species from being targeted by commercial and recreational anglers. White sharks continue to be caught on the east coast in the nets of the Natal Sharks Board (NSB), which operates a shark control program to protect beach users against shark attack (Cliff et al., 1988). Between 1984 and 1995 an annual average of 40 *C. carcharias* were caught in NSB nets, and 15% were released alive. This activity has formed the basis of a small-scale tagging program that has provided the first estimates of the size of the white shark population (Cliff et al., 1996b). Information about the distribution, diet, movements, and catches of *C. carcharias* in South Africa is available from Bass et al. (1975) and Cliff et al. (1989, 1996a).

Little is known about age and growth of *C. carcharias*, mainly because so few are caught at any one locality, thus hampering collection of vertebral samples for ageing purposes. Knowledge of age at maturity, maximum ages, and growth rates is a prerequisite for age-based methods of stock assessment, which in turn can be used for the management of this species. The only previous attempt at ageing the white shark was that of Cailliet et al. (1985) who had access to only 21 samples, mainly from California. This study attempts to provide age estimates for *C. carcharias* from South Africa from vertebral growth ring counts of 114 sharks.

[1] Stevens, J. D. 1997. CSIRO Marine Laboratories, Tasmania, Australia. Personal comm

Materials and methods

Sampling

Sharks were sampled in NSB nets from 1984 to 1995. Each net was 214 m long, 6 m deep, had a 50-cm stretched mesh, and was set in water 10–14 m deep, parallel to and 300–400 m from shore. For additional details of the netting operation see Cliff et al. (1988).

Precaudal length (PCL) was measured in a straight line from the snout tip to the precaudal notch and is used throughout this study, unless indicated otherwise. To compare our findings with those reported in the literature, the following equations were used to convert lengths:

$$Total\ length\ (TL) = 1.251\ PCL + 5.207$$

(n =36; range 131–307 cm PCL; 95% confidence limits on slope: 1.233 and 1.268; r^2=0.9984) (Cliff et al., 1996a); and

$$PCL = 0.8550\ TL - 0.0955$$

(n =58; range 96–447 cm PCL; 95% confidence limits on intercept: –0.130 and –0.061; r^2=0.996) (Mollet and Cailliet, 1996).

Lengths were converted by means of the method considered most appropriate.

Mass was determined by weighing each shark and subtracting the mass of gut contents where they exceeded 1 kg. Maturity was assessed by the criteria of Bass et al. (1973), where males were considered mature only if their claspers were fully calcified. In females, maturity was based on the presence of distinct ova in the ovary and uteri, which had expanded from a thin, tubelike condition to form loose sacs (Bass et al., 1973; Cliff et al., 1988). Vertebral samples were taken anterior to the origin of the first dorsal fin from 61 females (128–297 cm) and 53 males (142–373 cm). Mass range was 42–442 kg for females (n=60) and 46–882 kg for males (n=53). Vertebrae were stored frozen (60%) or in 70% isopropyl alcohol (31%), or dried (9%). Individual centra were cleaned by removing the connective tissue from the corpus calcareum with forceps. Dried samples needed additional soaking in a 5% solution of sodium hypochlorite for 20–40 minutes.

Ring counts

X-radiography was used to enhance the visibility of the growth rings. X-radiographs of whole centra were prepared on an Odel Pollux 700 generator with a Comet tube by using Agfa Ortho (Extremity) film and were processed with an Agfa Curix 160 processor. We x-rayed, using mostly oblique exposure, all centra with the corpus calcareum (Figs. 1A and 2A) facing the tube at a set distance of 100 cm. At 50 mA, exposure times ranged from 0.3 to 0.8 seconds and voltage from 28 to 34 kV. The x-radiographs were then scanned with an Agfa Arcus II scanner and Adobe photoshop software. Ulead ImagePals 2 GO! (Ulead Systems, 1992–94) and CorelDRAW! (Corel Corp., 1993) were used to enhance and work with the images.

A growth ring (GR) was defined as a band pair, composed of one calcified (opaque) and one less-calcified (translucent) band (Fig. 1A). The finer, narrower rings (circuli), also observed by Cailliet et al. (1985), were not used for ageing purposes. The angle change on the centrum face (Fig. 2A), a result of the difference between fast intrauterine and slower postnatal growth (Walter and Ebert, 1991), was regarded as the birth mark.

Counts were made directly from the x-radiographs (XRs) by one reader (A) and from the scanned images (SCs) by two readers (A and B). These three ways of viewing the vertebrae will be called methods XR-A, SC-A, and SC-B, for brevity. Each reader made three nonconsecutive GR counts, without knowledge of the shark's length and previous counts. Count reproducibility was determined by using the following four methods:

1 The average percentage error (APE) as described by Beamish and Fournier (1981) in which an upper limit in the APE was arbitrarily set at 20% for each vertebra (samples were discarded if, after a recount, they were still above this limit) and a final APE index was recalculated and an intrareader comparison (XR-A vs. SC-A) and interreader comparison (SC-A vs. SC-B) of APE values were then conducted;
2 The index of precision D (Chang, 1982);
3 The percentage agreement among the three counts for each method; and
4 The percentage agreement in paired GR counts between the methods.

Centrum analyses

Dorsal centrum diameter and dorsal "birth diameter" were measured in a transverse plane along a straight line through the focus of each vertebra (Fig. 2B). The dorsal "birth diameter" was marked on the x-radiographs and screen images. Distance from the focus to the outer edge of each GR (Fig. 2B) was measured on the scanned images by using CorelDRAW!

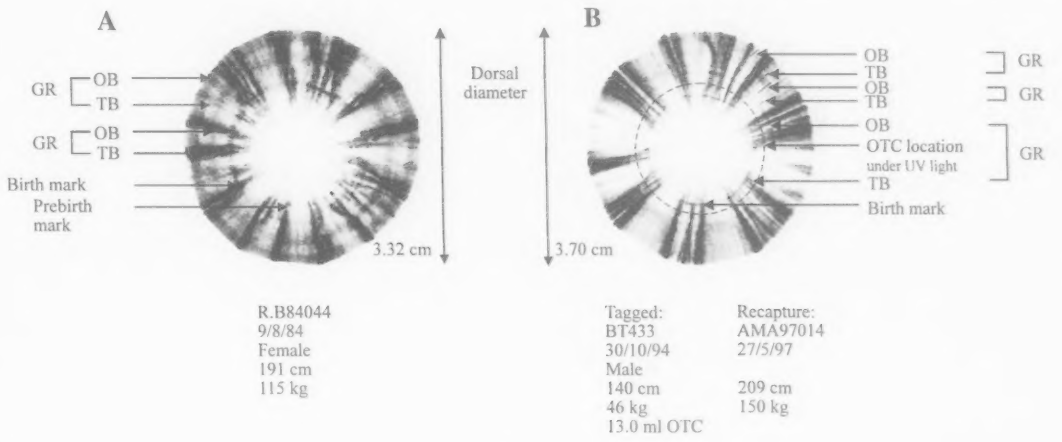

Figure 1

Inverted scanned images of x-radiographs of two white sharks. OB = opaque band, TB = translucent band, GR = growth ring.

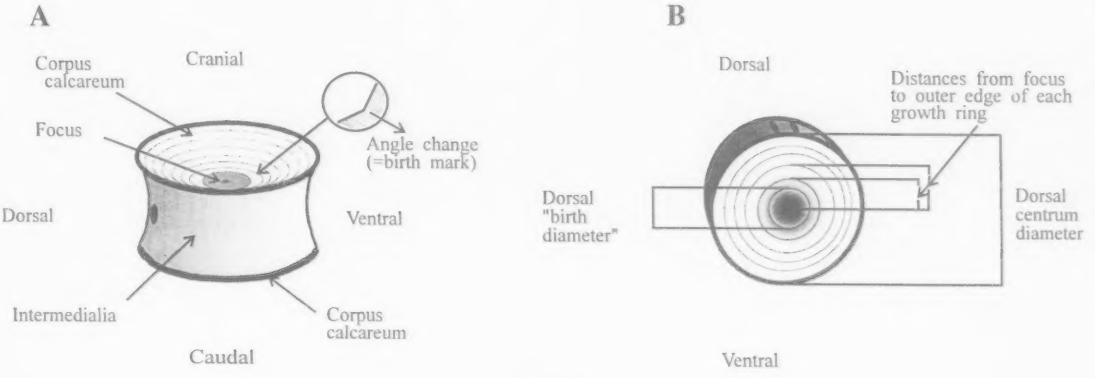

Figure 2

Schematic drawings of a vertebra illustrating terms used in the text.

The relationships between centrum diameter and both shark length and mass were examined by comparing regression lines of both sexes with the procedure of Zar (1974), which compares the slopes and elevations with Student's *t*-tests. Significance levels given in the text are the results of these tests. Outliers were determined by using Statgraphics (STSC, 1991) and eliminated.

The Dahl-Lea method of back-calculation (Carlander, 1969) was used, in which

$$PCL_t = CD_t\,(PCL_c/CD_c),$$

where PCL_t = length at GR t;
CD_t = centrum diameter at GR t;
PCL_c = length at capture; and
CD_c = centrum diameter at capture.

The Monastyrsky method of back-calculation (Bagenal and Tesch, 1978, cited by Francis, 1990) was used to estimate mass at age, in which

$$M_t = (CD_t/CD_c)^b\,M_c,$$

where M_t = mass at GR t;

M_c = mass at capture; and
b = the constant derived from the multiplicative regression of M on CD.

The constant b was derived by using the "body-proportional-hypothesis," where "if a fish at time of capture was 10 per cent smaller than the average fish with the same size of scale, the fish would be 10 per cent smaller than the expected length for the size of that scale throughout life" (Whitney and Carlander, 1956, cited by Francis, 1990).

Confirmation of the annual periodicity of GRs (Cailliet et al., 1983a, 1983b) was attempted with two methods of centrum analyses. First, the last deposited band was classified as translucent or opaque and related to the month of capture (Kusher et al., 1992). The observed and expected ratios of translucent to opaque last bands were then compared. Second, the marginal increment ratio (MIR) (Hayashi, 1976; Skomal, 1990) was calculated with the following equation:

$$MIR = (VR - R_n)/(R_n - R_{n-1}),$$

where VR = vertebral radius;
R_n = radius to the last complete GR; and
R_{n-1} = radius to the previously completed GR.

Mean MIR, with range and standard error, was then plotted against month.

In addition, 16 white sharks (between 1993 and 1995) were injected with oxytetracycline (OTC) solution (Engemycin, Intervet International B.V.), at a dose of 25 mg per kg body mass as recommended by Holden and Vince (1973) and McFarlane and Beamish (1987). Mass was estimated from the mass-length equation of Cliff et al. (1989). The OTC was administered in several places in the muscle around the first dorsal fin with a 15G × 1.5" disposable needle and 20-mL plastic syringe. Each shark was tagged with an orange identification tag (Hallprint PDA large plastic dart tag), labelled "tetracycline" and given a unique "BT" number.

Age and growth

The program PC-YIELD II (Punt and Hughes, 1989) was used to determine which of 10 different growth models provided the best fit to the data sets obtained by the three methods. Where appropriate, von Bertalanffy growth parameters (VBGP) were computed. The equation (von Bertalanffy, 1938) is

$$L_t = L_\infty (1 - e^{-k(t-t_0)}),$$

Table 1

Comparison of average percentage error (APE) indices and index of precision (D) for each method. Values are given before and after elimination of vertebrae with an APE > 0.2.

Methods	Preliminary APE index (%)	D (%)	n	Final APE index (%)	D (%)	n
SC-A	8.9	6.9	114	5.3	4.1	112
SC-B	12.9	9.8	114	5.4	4.1	108
XR-A	9.0	7.0	114	6.1	3.9	110

where L_t = length at GR t;
L_∞ = maximum theoretical length;
k = the rate at which L_∞ is reached; and
t_0 = the theoretical number of GR at length zero.

To determine whether GR deposition was related to an increase in mass rather than to time of year, Gompertz growth parameters were also calculated. The Gompertz equation (Silliman, 1967; Ricker, 1975) is

$$W_t = w_0 e^{G(1-e^{-gt})},$$

where w_t = mass at GR t;
G = initial exponential growth; and
g = exponential rate of decline.

Both growth equations were fitted by using the nonlinear regression procedure of STATGRAPHICS, which uses Marquardt's algorithm (Draper and Smith, 1981). Because this procedure is highly dependent upon initial estimates for the parameters, a wide range of initial parameters was used to prevent the models converging to a local minimum, i.e. converging to an unwanted stationary point of the sum of squares, rather than to a global minimum (Draper and Smith, 1981).

Results

Of the 114 processed vertebrae, between two and six, depending on the method, had an APE of over 20% after a recount and were discarded (Table 1). The final APE indices and D values showed little differences amongst methods, indicating similar reproducibility (Table 1). The percentage agreement among the three counts was high, e.g. with method SC-A, for 58.0% of the sample the three counts were the same (Table 2). In all three methods the majority of the readings was the same or differed only by one GR. For this reason, a mean of the three counts was

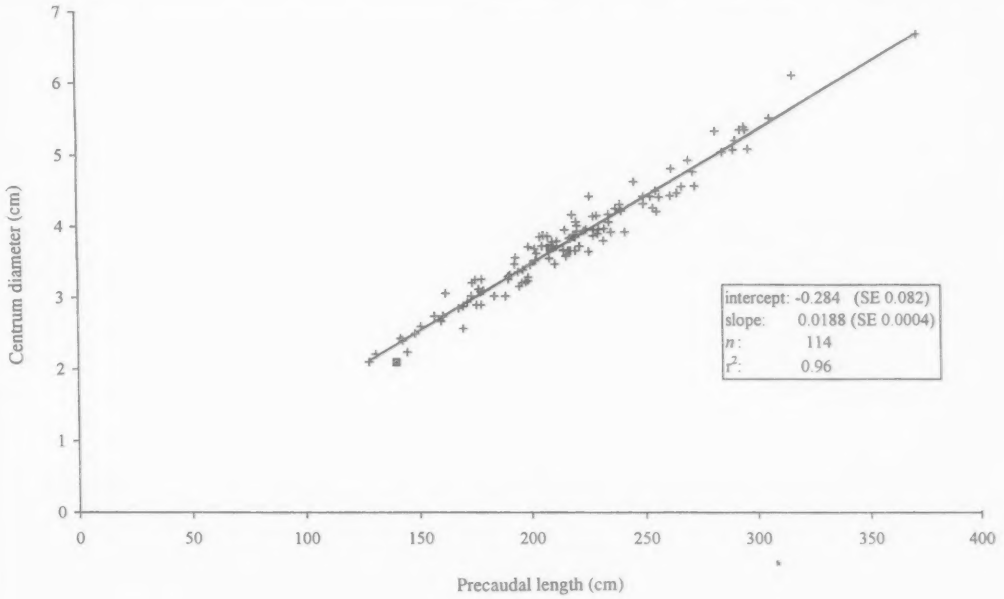

Figure 3

Relationship between centrum diameter and length for combined sexes of the white shark, *C. carcharias*. Squares indicate shark BT433 at tagging and recapture.

Table 2

Percentage agreement among the three counts for each method. Numbers in parentheses indicate sample sizes.

	Difference in GR counts					
Methods	0 GR	1 GR	2 GR	3 GR	4 GR	*n*
SC-A	58.0 (65)	33.0 (37)	7.1 (8)	0.9 (1)	0.9 (1)	112
SC-B	61.1 (66)	37.0 (40)	0.9 (1)	0.9 (1)	—	108
XR-A	50.0 (55)	36.4 (40)	11.8 (13)	1.8 (2)	—	110

Table 3

Percentage agreement in paired growth ring (GR) counts between methods. Numbers in parentheses indicate sample sizes.

	Difference between counts				
Methods	0 GR	1 GR	2 GR	3 GR	*n*
SC-A - SC-B	42.5 (45)	41.5 (44)	15.1(16)	0.9 (1)	106
SC-A - XR-A	59.6 (65)	34.9 (38)	4.6 (5)	0.9 (1)	109

taken as a GR estimate in all three methods and used for all further calculations. The two readers agreed on the mean GR estimate in 42.5% of the vertebrae; in 59.6% of the vertebrae there was no difference between GR estimates obtained by the same reader using the two methods (Table 3).

Centrum analyses

Prebirth marks were found in all vertebrae with method XR-A and in 33% of the vertebrae with method SC-A (Table 4). Using all three methods, we

Table 4

Percentage of vertebrae where prebirth marks were present and nature of the first band after the angle change.

	Prebirth marks		First band after angle change		
			opaque	translucent	
Method	%	*n*	%	%	*n*
SC-A	33	114	94	6	62
SC-B	—	—	96	4	97
XR-A	100	114	88	12	81

Table 5

Observed and back-calculated precaudal length (PCL) at number of growth ring for the white shark, *C. carcharias*. Growth ring estimates were obtained with method SC-A.

No. of growth rings	Observed PCL (cm)					Back-calculated PCL (cm)				
	Min	Max	Mean	SD	*n*	Min	Max	Mean	SD	*n*
0	131	131	131	—	1	85	118	100	7	114
1	128	178	156	16	12	96	182	133	17	112
2	161	228	192	19	18	121	221	165	22	99
3	172	236	204	17	25	150	241	191	24	77
4	197	265	225	16	26	169	270	212	25	46
5	215	291	246	22	15	184	261	222	21	22
6	238	297	276	21	7	212	271	240	18	13
7	263	307	287	19	4	233	294	264	19	10
8	282	293	288	8	2	259	301	279	18	5
9	—	—	—	—	—	278	308	289	16	3
10	317	317	317	—	1	300	335	317	24	2
11	—	—	—	—	—	325	325	325	—	1
12	—	—	—	—	—	338	338	338	—	1
13	373	373	373	—	1	350	350	350	—	1
14	—	—	—	—	—	369	369	369	—	1

found that the majority of the vertebrae had an opaque band as the first band after the angle change (Table 4). Only samples where the nature of the first band was the same in all three counts were considered for our analysis.

A statistically significant linear relation was found between centrum diameter and PCL (Fig. 3). There was no significant difference between the sexes in the slopes ($P>0.5$), but a significant difference between the elevations ($P<0.001$). Because the intercepts differed only by 0.02, no visual difference in the predicted values of females and males was perceptible, and the common intercept was used to plot a regression for the combined sexes. The intercept was close to zero; therefore no correction, such as the Fraser-Lee method (Carlander, 1969; Branstetter, 1987), was used.

One of the 16 white sharks injected with OTC (BT433) was recaptured after the completion of the study. The shark was tagged during a fishing competition on 30 October 1994; it measured 140 cm and weighed 46 kg. On recapture 942 days later, on 28 May 1997, it measured 209 cm (150 kg). The squares in Figure 3 indicate the length and centrum diameter of this shark at tagging, i.e. at the OTC marker and at recapture.

Because of the similarity of the above regressions for females and males, back-calculations were performed on combined sex data. Mean back-calculated lengths were lower than observed values (Table 5). Lee's phenomenon, a tendency for back-calculated lengths of older fish in the earlier years of life to be systematically lower than those of younger fish at the same age (Carlander, 1969; Smith, 1983), was evident, but not consistent. In sharks with 7 and 8 GRs, for example, the back-calculated values for each GR class were higher than those for sharks with 6 GRs.

A multiplicative relationship was found between centrum diameter and mass and no significant difference was found between the sexes in the slopes ($P>0.5$), but a significant difference between the elevations ($P<0.001$) (Fig. 4). Again, because of the similarity of the regressions for females and males, back-calculations were performed on combined sex data. Back-calculated mass was lower than observed values (Table 6). Lee's phenomenon was evident, but not consistent, and showed a similar trend to that of back-calculated lengths. Because of the use of mean GRs, the number of observed lengths (or masses) per GR class, plus the number of back-calculated lengths (or masses) in the next GR class, did not always add up to the total number of back-calculated lengths (or masses) of the previous GR class (Tables 5 and 6).

The observed ratio of translucent to opaque last bands differed significantly from the expected ratio (χ^2 test, $P<0.001$, $n=33$), irrespective of whether opaque band deposition was assumed to occur in summer or in winter. For this analysis only vertebrae were used where the nature of the last band was the same in all nine counts (i.e. in all three counts of all three methods). The exclusion of borderline cases, i.e. only summer months (22 Dec–20 Mar) and winter months (21 Jun–22 Sep), did not alter the result

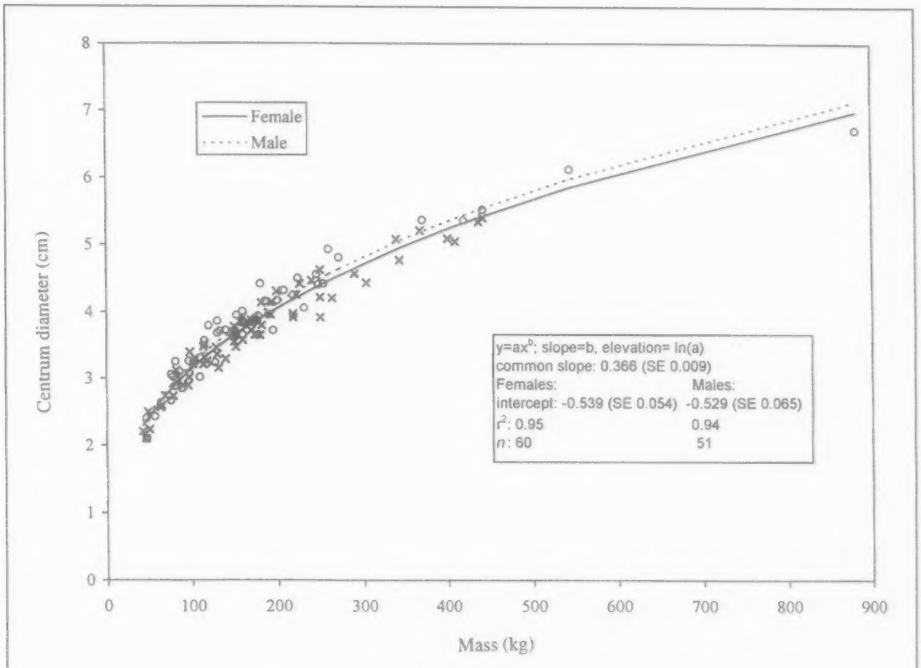

Figure 4

Relationship between centrum diameter and mass for female (x) and male (o) white sharks, *C. carcharias*. Squares indicate shark BT433 at tagging and recapture.

Table 6

Observed and back-calculated mass at number of growth ring for the white shark, *C. carcharias*. Growth ring estimates were obtained with method SC-A.

No. of growth rings	Observed mass (kg)					Back-calculated mass (kg)				
	Min	Max	Mean	SD	*n*	Min	Max	Mean	SD	*n*
0	42	42	42		1	14	36	22	4	112
1	46	97	69	19	11	18	120	48	17	110
2	68	199	120	37	18	33	198	85	31	98
3	81	218	139	35	25	55	256	124	44	76
4	98	250	176	42	26	73	352	164	55	46
5	112	368	234	68	15	90	280	188	48	22
6	218	442	314	84	7	186	313	239	42	13
7	272	442	386	77	4	238	416	310	55	10
8	371	437	404	47	2	351	406	380	23	5
9	—	—	—	—	—	420	504	452	45	3
10	544	544	544	—	1	506	625	565	84	2
11	—	—	—	—	—	618	618	618	—	1
12	—	—	—	—	—	685	685	685	—	1
13	882	882	882	—	1	751	751	751	—	1
14	—	—	—	—	—	859	859	859	—	1

(χ^2 test, $P<0.001$, $n=22$). With method SC-A, and again only with vertebrae where all three counts had the same last band, the observed ratio of translucent to opaque last bands differed significantly from the expected ratio (χ^2 test, $P<0.001$, $n=75$), again irrespective of whether opaque band deposition was

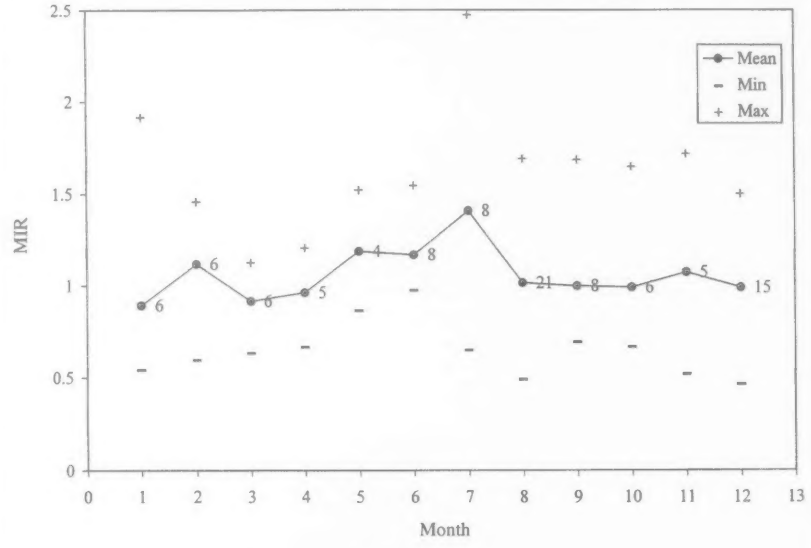

Figure 5

Marginal increment ratio (MIR) by month for the white shark, *C. carcharias*. Numbers indicate sample size, vertical bars indicate the standard error of the mean, and +/– indicates the range. Measurements were obtained by using method SC-A. 1 = January, 12 = December.

assumed to occur in summer or in winter. The exclusion of borderline cases, however, resulted in a significant difference between observed and the expected ratios (χ^2 test, $P<0.001$, $n=39$), assuming opaque band deposition in summer, but no significant difference (χ^2 test, $P>0.05$, $n=39$), assuming a translucent band deposition in summer.

The vertebra of shark BT433 was difficult to read (Fig. 1B), when compared with other sharks of similar length and mass (Fig. 1A). For this reason, we also examined the vertebra with transmitted light (Wintner and Cliff, 1996), and our interpretation of GRs is based mainly on this method. The OTC marker was visible in the opaque band (injected 30 October 1994). The deposition of OTC when injected intramuscularly occurs after a couple of weeks (Holden and Vince, 1973) or 21–35 days (Brown and Gruber, 1988). The opaque band would therefore have been deposited in summer (November or December). The last band in the vertebra was an opaque band. Because the shark was recaptured on 27 May 1997 (the beginning of winter), the translucent band might have been in the process of being formed.

MIR analysis of the entire sample (Fig. 5), however, did not show a distinct time of GR formation because mean and minimum ratios did not get close to zero. The results of a Kruskal-Wallis analysis indicated that there is no relation between MIR and month ($P=0.39$). In view of the results from the above recaptured shark and if the peak in July was regarded as a single peak, we assumed that one GR was formed annually, combined with the minimum MIR trend. With the latter, GR formation may occur during December or January. Because of the ambiguity of the results of the centrum analyses, however, annual periodicity of GR could not be confirmed.

Age and growth

The von Bertalanffy growth function was the most appropriate model for the data sets obtained by both methods SC-A and XR-A. The length-GR data set obtained by method SC-B was not investigated further because two growth models, Putter no. 2 and Gompertz (Punt and Hughes, 1989), provided a better fit than did the von Bertalanffy growth function. In addition, the L_∞ values obtained by the two models were too low to be realistic according to observed sizes of white sharks. Sexes could not be compared because there were no females larger than 300 cm; consequently no meaningful von Bertalanffy growth function could be fitted. Although the VBGP for the two methods SC-A and XR-A differed, there was little difference in the calculated GR over the range of lengths sampled (Fig. 6). Method SC-A had lower relative standard errors and a more realistic L_∞ than

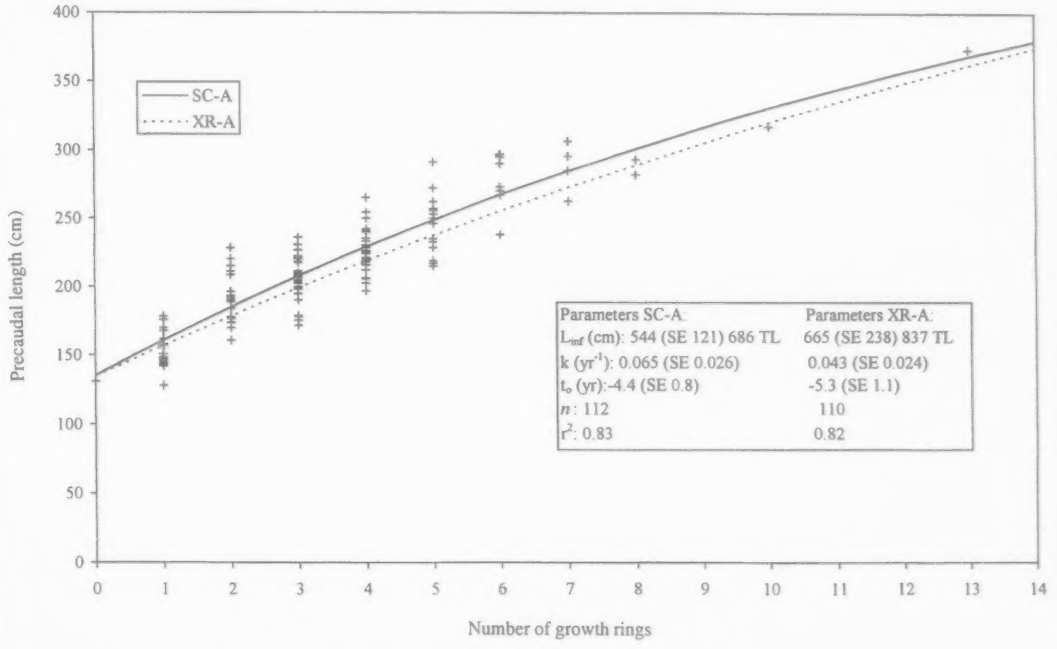

Figure 6

Von Bertalanffy growth curves and parameters for the white shark, *C. carcharias*, sexes combined. Growth ring estimates were obtained by using methods SC-A and XR-A. Observed values (+) are those for the method SC-A. Squares indicate shark BT433 at tagging and recapture.

method XR-A. For these reasons the results of the former method were used for back-calculations, MIR analysis, fitting of the Gompertz growth curve, growth calculations, and GR estimates.

Table 7 shows the number of GRs counted for various animals. The largest female, an adolescent, (297 cm) had 6 GRs; there were no mature females. Of the three mature males, the smallest had 8 GRs (293 cm), the other two had 10 and 13 GRs (317 and 373 cm), respectively. Size at birth ranged between 100 cm (back-calculated value) and 135 cm (predicted value). Shark BT433 was found to have one GR at tagging (140 cm) and three GRs at recapture (209 cm), after 2.6 yr at liberty (Fig. 1B; Fig. 6).

Table 7

Growth ring (GR) counts for animals of certain lengths (PCL, cm) or certain mass (kg).

	Male			Female		
	No. of GRs	PCL	mass	No. of GRs	PCL	mass
Lowest number of GRs	1	142	56	0	131	42
Highest number of GRs	13	373	882	8	282	437
Smallest animal	1	142	46	1	128	42
Largest animal	13	373	882	6	297	442
Smallest mature animal	8	293	371	—	—	—

A Gompertz growth curve was fitted to the mass-GR data (Fig. 7). The female and male with the highest number of GRs, had 8 GRs (437 kg) and 13 GRs (882 kg), respectively (Table 7). Mass at birth ranged between 22 kg (back-calculated value) and 54 kg (predicted value).

Mean growth rates calculated from observed lengths were higher overall than those calculated from predicted lengths (Fig. 8). Mean growth for predicted lengths was 26 cm for the period 0–1 GR, decreasing to 20 cm (4–5 GRs), 16 cm (7–8 GRs), and 12 cm (12–13 GRs). Mean observed growth in mass was also higher than that of predicted values (Fig. 8). Mean growth for predicted mass was 23 kg for 0–

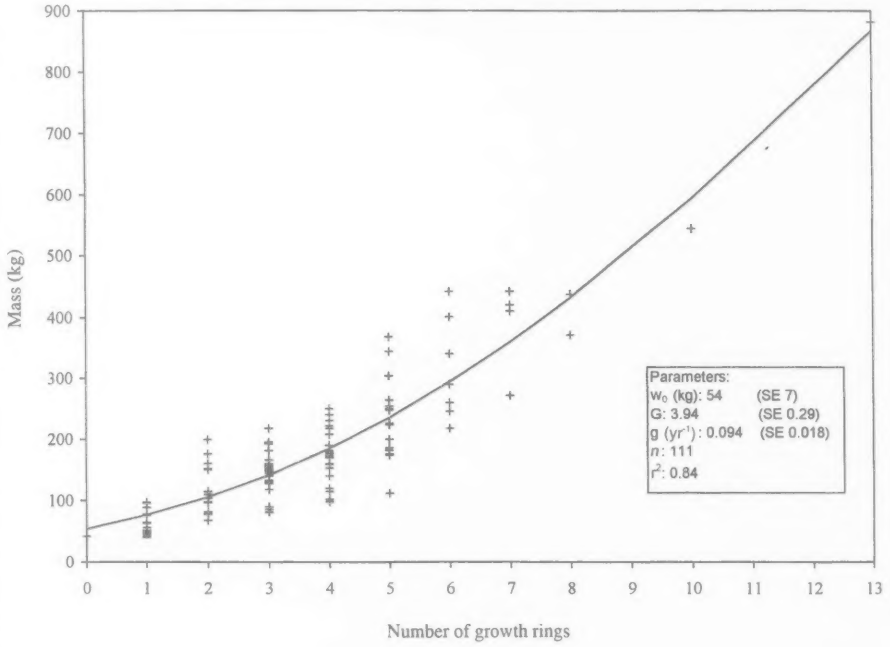

Figure 7

Gompertz growth curve for the white shark, *C. carcharias*, sexes combined. Growth ring estimates were obtained by using method SC-A. Squares indicate shark BT433 at tagging and recapture.

1 GR, increasing to 51 kg (4–5 GRs), 78 kg (7–8 GRs) and 94 kg (12–13 GRs). Shark BT433 grew 69 cm and 104 kg in 2.6 years (Fig. 1B) which represents a mean annual growth of 27 cm and 40 kg.

Discussion

Annual GR periodicity has been partly verified for several species (Cailliet, 1990). For some species of the family Lamnidae, biannual GR periodicity has been reported. Parker and Stott (1965) used the mean length of 17 *Cetorhinus maximus* sampled in winter and 15 sampled in summer and treating them as age classes, derived a tentative growth curve. They stated that their growth curve derived from ring counts of five vertebrae was similar to the first one when a deposition of two GRs per year was assumed. They were, however, careful to note that there was "nothing to indicate beyond doubt that the addition of two rings is the direct result of the passage of an annual seasonal cycle" and said that several findings did not "harmonise with the idea of annual increase of two rings."

Pratt and Casey (1983) determined age and growth of *Isurus oxyrinchus* from the Atlantic by length-month analysis, length-frequency analysis, tag-recapture information, and vertebral ring counts. The results of the first analysis were used to interpret the accuracy of the other methods. Their growth curve for *I. oxyrinchus*, based on back-calculated sizes, agreed closely with those obtained by the other methods if biannual ring deposition was assumed. The vertebrae from four noninjected recaptured *I. oxyrinchus*, however, gave inconclusive results because two supported annual and the other two biannual GR deposition. Pratt and Casey stated that "vertebral rings may thus yield an approximation of age, accurate in the smaller sizes where estimates have been correlated with other methodologies. Adults may not lay down yearly, and it is possible that we have underestimated their age, but we have no data to support this possibility."

Cailliet et al. (1983a) assumed annual GR deposition in *I. oxyrinchus* from California waters. Their growth rate estimates, based on tag-recapture analysis, were therefore half of those of Pratt and Casey (1983) and had a much smaller variation in the estimate. Cailliet et al. (1983a) stated that although "this discrepancy could be related to differences in habitat or environmental conditions or differences in

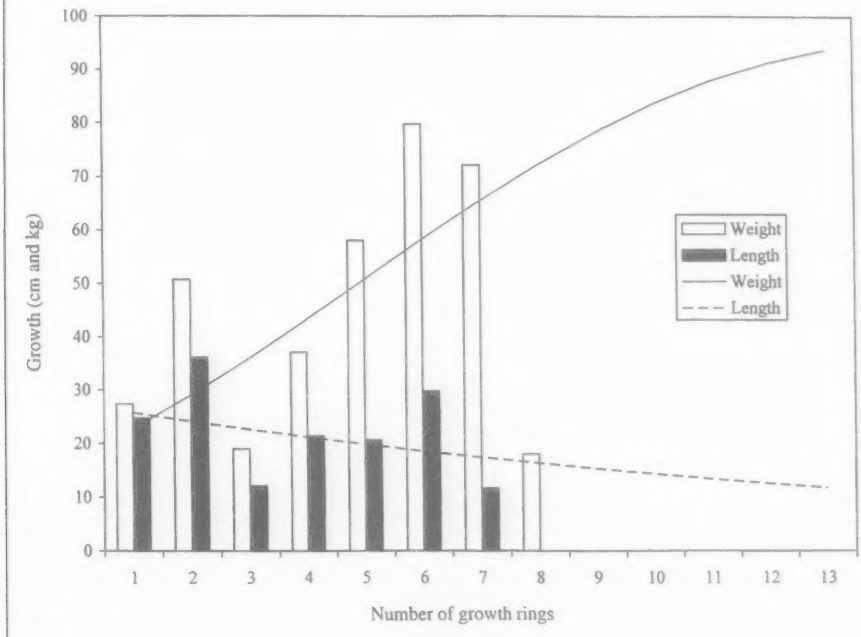

Figure 8

Observed (bar) and predicted (line) growth in mass and length per growth ring for the white shark, *C. carcharias*. Growth ring estimates were obtained by using method SC-A.

sample size or ageing methodology" it was interesting to note "that the growth rate reported by Pratt and Casey (1983) based on their back-calculation from counts of bands on centra, would be similar to ours if each pair of bands from their fish were interpreted as an annual event."

Cailliet et al. (1985) assumed annual GR periodicity in their age and growth study of *C. carcharias*. As with the studies mentioned above, MIR analysis could not be included to validate the temporal periodicity of the GRs. The only lamnoid study to have done so, apart from this one, was that of Branstetter and Musick (1994) on *Carcharias taurus*, which suggested a semiannual periodicity of band and ring formation. However, samples from three winter months were lacking. They also used a "odd-even ring count analysis" to verify this suggestion.

The results of the MIR analysis (Fig. 5) were inconclusive and did not confirm the results from shark BT433. Considerable time was spent on this analysis and great care was taken to discern the last deposited band in order not to overlook a recently formed band. Several vertebrae were remeasured, resulting only in removing the peaks of the curve and not in a reduction of the minimum MIR. Examination of the relative frequency of vertebrae with large MIR to those with low MIR plotted against month (Batista and Silva, 1995) did not shed light on this issue. Annual or biannual GR periodicity for *C. carcharias* could not be confirmed in this study by two centrum edge analyses.

There seems to be some unexplained variation in GR deposition among lamnoids, which is further compounded by our study. Pratt and Casey (1983) stated that in *I. oxyrinchus* instead of the traditional annual ring deposition "a more likely cause for ring formation would be times of stress or deprivation such as migration and mating." Similarly, Branstetter and Musick (1994) suggested that in *C. taurus* the formation of semiannual bands may reflect their north-south seasonal migration pattern, which is prompted in part by changing light and temperature patterns. There is currently not enough evidence to prove a similar migration pattern for *C. carcharias* in South African waters (Cliff et al., 1996a, 1996b).

Traditionally, ages of sharks have been related to length (Cailliet et al., 1983b; Cailliet et al., 1986). Natanson and Cailliet (1990) found that band deposition in *Squatina californica* was not annual but related to somatic growth. We therefore decided to fit a Gompertz growth curve because this curve usually describes the relationship between mass and age

well (Ricker, 1975). The curve did not show the typical asymmetrical sigmoid curve but seemed to approach an upper asymptote (Gulland, 1983). It was the method with the lowest relative standard errors for all parameters. Although there is also considerable variation in mass at GR, we felt that the Gompertz growth curve has merit, especially because there is a large change in mass associated with a small increase in length among large sharks. The results of the MIR analysis could be interpreted such that GR formation is not related to time of year but to mass increase (some sharks taking a longer time than others to gain the same amount of mass).

Typically, opaque band deposition is associated with summer growth (Cailliet et al., 1983b, 1986; Kusher et al., 1992), and the nature of the last deposited band can be related to the month of capture to verify this. Using method SC-A and only summer and winter months, we found that the observed ratio of translucent to opaque last bands did not differ significantly from the expected ratio, assuming a translucent band deposition in summer. When we used nine ring counts, however, the analysis did not show any relation between the nature of the last band and season. The analysis could be considered statistically weak owing to the low sample size but was included to emphasize the accuracy of the last band identification. In this study the band immediately after the angle change was opaque in most vertebrae, which is in keeping with Francis (1996) who reported time of parturition of white sharks as spring or summer. In addition, if our interpretation of vertebral bands in shark BT433 is correct, the opaque band would be formed in summer. Because of the inconclusive results of the centrum analyses of the entire sample, however, more recaptures of sharks injected with OTC are needed to confirm this theory.

The relation between centrum diameter and shark length was linear, as was found in *C. carcharias* by Cailliet et al. (1985) and in several other shark species (Cailliet et al., 1983b; Schwartz, 1983; Branstetter, 1987). For another species of the family Lamnidae, *I. oxyrinchus,* Pratt and Casey (1983) found a slightly curvilinear relationship for both females and males. The relation between centrum diameter and mass was multiplicative, which explains the slightly bigger difference in centrum diameter between the sexes than in the relation between centrum diameter and length. The differences between the sexes in both relationships, however, are slight and are probably not of biological significance.

Back-calculated mass and length values were lower than observed values. The differences between mean observed length (or mass) and mean back-calculated length (or mass) at each GR would decrease substantially if the observed GR 0 were treated as GR 1. This could be an indication that the angle change of the corpus calcareum is not formed at birth but in the first summer growth (Brown and Gruber, 1988; Wintner and Cliff, 1996).

X-radiography to enhance the visibility of GRs in elasmobranch vertebrae has been used successfully on several species (Cailliet et al., 1983a, 1983b; Yudin and Cailliet, 1990; Ferreira and Vooren, 1991). This technique was also used in the only other ageing study of *C. carcharias* by Cailliet et al. (1985). They counted GRs directly from x-radiographs and used silver nitrate staining to corroborate counts of larger vertebrae that proved more difficult to read. In our study, scanned images allowed for easy and rapid counts of rings and measurements for back-calculations. In addition, scanned images were easier to interpret because they showed less detail of the narrow circuli and prebirth marks than did the x-radiographs.

Prebirth marks in placental species are normally attributed to the time of placenta formation and attachment (Casey et al., 1985; Branstetter, 1987; Branstetter and Stiles, 1987). In our study, prebirth marks were found in *C. carcharias* vertebrae. No comments on prebirth marks in *C. carcharias*, *I. oxyrinchus,* or *Alopias vulpinus* were made by Cailliet et al. (1985), Pratt and Casey (1983), and Cailliet et al. (1983a), respectively. Branstetter et al. (1987) did not find prebirth marks in *Galeocerdo cuvier*, another aplacental species. Branstetter and Musick (1994), however, found prebirth marks in their *Carcharias taurus* specimens and related the first consistent prebirth ring to the size of the embryo when digestion of the large quantities of eggs begins. We did not relate prebirth marks to embryonic length using back-calculations because they represent growth in utero.

The APE indices for the three methods (5.3–6.1%) were considered acceptable. They were lower than those of the four methods used by Wintner and Cliff (1996) for *Carcharhinus limbatus* (8.1–13.0%, n=80–87) and those of Cailliet et al. (1990) who used "bow tie" sections of *Mustelus manazo* (6.9–12.7%, n=28–30). D-values (3.9–4.1%) were also considered to be acceptable because they were similar to those of Natanson and Kohler (1996) for *C. obscurus* (3,3%, n=42) and lower than those of Cailliet et al. (1990) (6.8–12.7%, n=27–30).

Age and growth estimates

Only one shark injected with OTC was recaptured (BT433). Although it was at liberty for an adequate time period, an interpretation of the bands on the x-radiograph was difficult, and therefore the results were based mainly on viewing the vertebra with

transmitted light. The number of GRs counted, however, were the same with these two methods and for both authors. While at liberty, the shark's mean annual growth increment was 28 cm and 42 kg. Francis (1996) reported size at birth between 92 and 116 cm and weight at birth between 12 and 32 kg and given that this shark was 140 cm and 46 kg at tagging, it is reasonable to assume that its age was in the region of one year. This estimation was confirmed by the OTC marker being visible at the edge of the first GR (Fig. 1B).

Table 8

Comparison of von Bertalanffy growth parameters. The bold values were obtained by refitting the data.

	Our study (SC-A)	Cailliet et.al (1985)	
		Their results	Refitted excluding 3 large animals
Range PCL	128–373	110–434	110–394
Range TL	165–472	129–508	129–461
VBGP			
L_∞	544 (686 TL)	653 (764 TL)	569 (666 TL)
SE	121	**134 (157 TL)**	110 (129 TL)
k	0.065	0.058	0.072
SE	0.026	**0.023**	0.028
t_0	–4.4	–3.5	–3.3
SE	0.8	**0.72**	0.72
n	112	21	18
r^2	0.83	**0.98**	0.97

Because we counted three GRs at recapture, the mean predicted growth/GR in the period from 1 to 3 GRs was 24 cm/GR and 33 kg/GR (Fig. 8). Assuming that one GR is deposited per year, the total growth of shark BT433 would be 62 cm and 86 kg in the period of 2.6 years. If the GR deposition is biannual, which is not impossible given the difficulty in interpreting this vertebra (Fig. 1B), the mean predicted growth would be 18 cm/GR and 32 kg/GR; this would amount to a total growth in a period of 2.6 yr (5.2 GR) of 94 cm and 166 kg. Because BT433 grew 69 cm and 104 kg, the first of these two predictions fits the observed growth better than the second.

Further evidence to support the hypothesis of annual GR deposition can be found in Figures 6 and 7. If the number of GRs represents years, the expected size and mass of shark BT433 at tagging and recapture after 2.6 years is in accordance with the observed values of our sample (Fig. 6). Assuming biannual GR deposition, we believe the shark's size and mass at tagging is still in accordance with the observed values (Fig. 7); however, it would have been in the region of 288 cm and 375 kg at recapture. Because evidence of annual GR deposition in *C. carcharias* is based on the recapture of a single shark injected with OTC and because our centrum analyses neither confirmed nor contradicted annual ring deposition, the discussions below are based on number of GRs rather than years.

Our VBGPs, in the absence of very large sharks, were L_∞ = 544 cm (SE 121), k = 0.065/yr (SE 0.026), and t_0 = –4.4 yr (SE 0.8). We fitted a von Bertalanffy growth curve to the data points presented by Cailliet et al. (1985) in order to compare standard errors (Table 8). The results were very similar, but given the larger sample size in our study, it would appear that there is greater variation in length at number of GRs in *C. carcharias* from South Africa.

Our largest shark (373 cm) measured 452 cm TL. The absence of larger sharks in our study undoubtedly accounts for the lower L_∞ of 544 cm (686 cm TL), as opposed to that of Cailliet et al. (1985) of 654 cm (764 cm TL). This finding was confirmed when the three markedly larger sharks (494–508 cm TL) of their study were omitted and the recalculated L_∞ was 569 cm (666 cm TL) (Table 8). The conversion of the original data of Cailliet et al. (1985) from TL to PCL had no effect on the VBGP and their standard errors. One should keep in mind, however, that comparisons of L_∞ are somewhat hampered by the fact that TL length is measured in two different ways (Mollet et al, 1996) by various authors, although the difference in *C. carcharias* is not as pronounced as, e.g., in members of the family Carcharhinidae.

The maximum size attained by the white shark is the subject of much interest and controversy and, more importantly, uncertainty (Ellis and McCosker, 1991). Randall (1973, 1987) refuted the lengths of 1113, 900, and 640 cm TL attributed to *C. carcharias*. According to him, the largest reliable measured white shark is 513 cm (600 cm TL). Mollet et al. (1996) calculated the size of two large white sharks, using three morphometric measurements, at 453–701 cm (530–820 cm TL) and 393–598 cm (460–700 cm TL), respectively. These results were consistent with the estimated TL of >700 and 700 cm, respectively. They concluded that the most solid TL estimates for these two sharks were those original estimates. Our L_∞ is larger than the shark from Randall and is smaller than the data of Mollet et al. (1996) and Cailliet et al. (1985).

Our growth coefficient is similar to that found by Cailliet et al. (1985), and both are an order of magnitude lower than that of *I. oxyrinchus* at 0.203–0.266 (Pratt and Casey, 1983) and that of *Lamna nasus* at 0.116 (Aasen, 1963). In the first year of growth, *C. carcharias* grows 19–26% of its size at birth which is less than that of other lamnoids (Branstetter, 1990). Our findings place *C. carcharias* in Branstetter's (1990) group of sharks with slow growth (k<0.10; growth in the first year<30% of the birth size).

In our study, back-calculated size at birth was 100 cm and calculated value was 135 cm. The smallest accurately measured free-swimming *C. carcharias* in southern Africa was 108 cm (140 cm TL) (Smith, 1951) and the sizes of the smallest white sharks caught at the NSB are 128–145 cm. "Umbilical scars" (Cliff et al., 1996a) were present in sharks of 138, 143, 144, and 145 cm, including the 131 cm (0 GR) specimen of this study. If the presence of these scars is interpreted as an indication of recent birth, it is tempting to suggest a very wide range in size at birth, between 100 and 145 cm. These scars, however, may persist for some time after birth and given a growth of about 25 cm/yr in newborn sharks, birth size of *C. carchirias* would be more in the region of that reported by Francis (1996), i.e. 92–116 cm (120–150 cm TL). Our range in mass at birth (22–54 kg) is also substantial, which is in keeping with Francis (1996) who stated that the range in mass at birth for *C. carcharias* is quite pronounced.

Our three mature males had 8, 10, and 13 GRs (293, 317, and 373 cm; 371, 544, and 882 kg, respectively). The NSB has caught immature specimens larger and heavier than our smallest mature, e.g. a 295 cm (420 kg) and a 306 cm (442 kg) specimen (Cliff et al., 1996a). Pratt's (1996) smallest mature male was 299 cm (379 cm TL), which is similar to our shark; however, he notes that sizes at sexual maturity for male *C. carcharias* vary widely in the literature. These differences could be due to a variation in length at maturity depending on location, both compounded by the use of different length conversion equations and maturity criteria. If the number of GRs is taken as an age estimate, assuming annual GR deposition, male *C. carcharias* in South Africa would mature between 8–10 years which is similar to the findings of Cailliet et al. (1985) who worked with a size at maturity of 313–365 cm (366–427 cm TL), corresponding to an age of 9–10 years. This age at maturity is higher than that of other lamnids, e.g. that of male *I. oxyrinchus* at 2–3 years (Pratt and Casey, 1983) and male *L. nasus* at about 5 years (Paust and Smith, 1986).

No mature female has ever been examined from NSB nets, and the biggest female in our study was 297 cm (6 GRs). The biggest female on record is an immature 348 cm specimen (Cliff et al., 1989), and Bass et al. (1975) reported a mature female of 352 cm (445 cm TL). Again if GRs are deposited annually, the above specimens would be 11 and 12 years, respectively. Age at maturity for female *C. carcharias* in South Africa would then be at least 12–13 years, slightly higher than that for males. Again, this age at maturity is higher than in other lamnids, e.g. that for female *I. oxyrinchus* at 7 years (Pratt and Casey, 1983) and female *L. nasus* at 9–10 years (Paust and Smith, 1986).

Although this study could not conclusively prove annual or biannual GR periodicity, the recapture of one shark injected with OTC provided some evidence for annual GR deposition. Assuming that only one growth ring is laid down per year, then *C. carcharias* from South Africa is relatively slow growing in comparison with other lamnoids. This observation would support current protective legislation. The NSB nets are now the only directed source of apparent fishing mortality for *C. carcharias* in South Africa. Cliff et al. (1996b) were of the opinion, using their estimates of mortalities, that the current fishing mortality did not represent overfishing of the white shark stock. Examination of interannual catch rates of *C. carcharias* in the NSB nets showed an significant decline immediately following the introduction of netting, but thereafter (1978–93) there was no significant change (Cliff et al., 1996a). Because they are apex predators, *C. carcharias* are likely to have a small population size (Cliff et al., 1996b), and we have no knowledge about the fecundity and nursery grounds of this species in South African waters. Any possible relaxation of the South African current legislation will depend on improved knowledge about population size, immigration and emigration, natural mortality, and fecundity of *C. carcharias* from South Africa.

Any such relaxation, however, is highly unlikely given the increasing protection that has been granted to this species worldwide. It is now also protected in some states of America (Fergusson et al., in press) and Australia (Stevens[1]), where such legislation is based on a more limited knowledge or understanding of the biology and population dynamics of this species.

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Estimation of instantaneous rates of tag shedding for school shark, *Galeorhinus galeus*, and gummy shark, *Mustelus antarcticus*, by conditional likelihood

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Abstract.—Fish and other animals are often tagged to estimate their abundance as well as rates of growth, fishing mortality, natural mortality, and movement. Results of these studies are biased if tags are not retained permanently and if tag loss is not taken into account. In this paper, we develop a simple tag shedding model to account for the effects of time at liberty, sex, and other factors and use one of its special cases to estimate the instantaneous tag shedding rate from data based on two double-tagging experiments on the school shark, *Galeorhinus galeus*, and gummy shark, *Mustelus antarcticus*, off southern Australia. For either species, tag shedding rate could vary with tag type, position of tag on fish, and sex of fish, but not with length at release or time at liberty. The shedding rate of Petersen disc fin tags was well above 50%/yr. Dart tags were shed at a higher rate (41%/yr for school shark; 63%/yr for gummy shark) than either "Roto" or "Jumbo" fin tags (8%/yr for school shark; 6%/yr for gummy shark). For either species of shark, the shedding rate of dart tags anchored in the basal cartilage of the dorsal fin was about half that of dart tags anchored in the dorsal musculature.

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Tags are markers placed on or in animals to identify an individual. Animals are tagged to estimate their abundance as well as rates of growth, fishing mortality, natural mortality, and movement. In many studies, a tagged animal is assumed to retain its tag permanently. This assumption, however, is not valid for certain types of tags. Consequently, many attempts have been made to estimate tag shedding rates (e.g. Davis and Reid, 1982; Francis, 1989; Faragher and Gordon, 1992; Treble et al., 1993; Hampton, 1996; Xiao, 1996a).

Tag shedding models are of three main types; all are based on Beverton and Holt's (1957, p. 205, equations 14.32–14.37) model for a double-tagging experiment. Some models are conditional on the number of recaptured fish with a single tag, as well as the number of recaptured fish with both tags as a function of time at liberty, and use the least squares method (Gulland, 1955, 1963; Chapman, 1961; Paulik, 1963; Chapman et al., 1965; Bayliff and Mobrand, 1972; Russell, 1980; Kirkwood, 1981; Alt et al., 1985) or more generally the maximum likelihood method (Robson and Regier, 1966; Seber, 1973; Seber and Felton, 1981; Wetherall, 1982; Kremers, 1988; Fabrizio et al., 1996) for estimation of parameters. Other models are conditional on the number of recaptured fish retaining at least one tag as a function of time at liberty and on the exact times at liberty (Wetherall, 1982). Use of these types of models in data analysis requires grouping recaptured fish by time at liberty because of an insufficient number of recaptures for a particular (exact) time at liberty, especially in small-scale tagging experiments. Still other models are conditional only on the exact times

at liberty (Kirkwood and Walker, 1984; Hampton and Kirkwood, 1989; Hearn et al., 1991; Xiao, 1996a). These models 1) use the exact times at liberty in model fitting, 2) use probabilities of tag retention directly rather than using the often statistically undesirable ratios as the dependent variable in regression analysis, 3) apply to both small (but see below) and large numbers of recaptures, and 4) yield estimates of tag shedding rates independent of instantaneous fishing mortality, natural mortality, and mortalities due to all other causes. Almost all previous tag shedding models have considered only the effects of fish time at liberty on shedding rates, ignoring effects of other equally or potentially more important factors, such as fish sex and size.

School shark *Galeorhinus galeus* (Linnaeus) and gummy shark *Mustelus antarcticus* (*sensu* Last and Stevens, 1994) are major species in the Australian southern shark fishery—a commercial fishery that extends from Western Australia through South Australia to Bass Strait and Tasmania in the east and that has an annual landed value of $A15.6 million (Walker et al., 1996). Two tagging studies were undertaken to study the growth (Moulton et al., 1992), natural mortality (Grant et al., 1979), and local movements of these two species within Bass Strait and off eastern Tasmania (T. I. Walker, Marine and Freshwater Resources Institute, PO Box 114, Queenscliff, Vic 3225 Australia, unpubl. data). These studies suggest that school shark are highly migratory, compared with gummy shark, but they provide little quantitative information about their rates of movements beyond these areas, where most sharks were tagged and released. Also, fishing effort was too poorly documented at the time of Grant et al.'s (1979) tagging program (1940s and 1950s) to be adequate for quantifying the rates of movement for these two species. Finally, predominant use of gill nets with large mesh sizes (8 inches) off the southern coast of Western Australia and off South Australia at the time of T.I. Walker's tagging study (1970s) led to a low level of fishing effort and a small number of recaptures. Such a lack of quantitative information on rates of movement hampered stock assessment. Consequently, a large-scale tagging experiment was designed (Xiao, 1996b) and implemented to fill in this gap. In that study, thousands of individuals were released; each individual was tagged with an easily attachable and highly visible external tag (a Roto tag or a dart tag), the shedding rate of which was to be determined through an accompanying double-tagging experiment (see below).

In this paper, we develop a simple tag shedding model to account for the effects of fish sex, size, and factors other than time at liberty and use a special case to estimate the instantaneous tag shedding rate for the two species of sharks.

Materials and methods

Tagging experiments

Two double-tagging experiments were performed on *G. galeus* and *M. antarcticus*. In the first experiment (Olsen, 1953; Walker, 1989; Table 1), a total of 2597 school and 363 gummy sharks with a respective total length range of 31–164 (85 ±43, n=2586) cm and 32–179 (102 ±24, n=362) cm were captured by longline hooks, measured to the nearest centimeter, tagged with an internal and external tag, and released in inshore waters off Victoria, South Australia, and Tasmania, Australia, from 22 May 1949 to 10 July 1954. Internal tags were either 50 mm long and 23 mm wide (J-tag), or 50 mm long and 22 mm wide (L-tag), or 35 mm long and 10 mm wide (S-tag) and were inserted into the body cavity through an incision on the left flank parallel to the muscles in the lower half of the body immediately below the posterior half of the first dorsal fin. External tags were a white (W-tag) or gray Petersen disc (G-tag); both were 16 mm in diameter and 1 mm thick and were placed in the midcentral part of the first dorsal fin. Of those released, 417 school and 20 gummy sharks were recaptured within 42.5 years. Their respective total length at recapture ranged from 43 to 175 (127 ±35, n=267) cm and from 83 to 152 (125 ±19, n=12) cm; their respective times at liberty ranged from 31 to 15,510 (2761 ±2758, n=417) d, and from 52 to 3900 (1771 ±1159, n=20) d.

In the second double-tagging experiment (Table 2), as part of a major tagging experiment (see above), 291 school and 731 gummy sharks with a respective total length range of 38–168 (134 ±17, n=291) cm and 40–176 (108 ±20, n=729) cm were captured in gill nets, measured to the nearest millimeter, tagged with two external tags (a Roto tag and a dart tag) either in the lower half or basal cartilage of the first dorsal fin, and released off southern Australia, from 15 December 1993 to 24 April 1996. Two types of Roto tags were used: either a 45-mm-long and 18-mm-wide Jumbo (Roto) tag, or a 36-mm-long and 9-mm-wide Roto tag (Daltons of New South Wales, Australia). The dart tag was 95 mm long and 2 mm in diameter (Hallprint of South Australia, Australia). As of 1 May 1997, 48 school and 207 gummy sharks were recaptured. Their respective total length at recapture ranged from 85 to 179 (135 ±18, n=38) cm and from 66 to 167 (115 ±17, n=150) cm; their respective times at liberty ranged from 31 to 633 (269 ±163, n=48) d, and from 1 to 1138 (275 ±244, n=207) d.

Table 1

Description of the first double-tagging experiment for gummy and school sharks. The number of recaptures includes, consecutively and in parentheses, that with two tags, with tag A only, and with tag B only. "—" indicates unknown or not computable.

Row	Species	Tag A	Tag B	Sex	Number released	Mean length at release (cm)	Length range at release (cm)	Number recaptured	Mean length at recapture (cm)	Length range at recapture (cm)	Mean time at liberty (d)	Range of time at liberty (d)
1	gummy	L-tag	W-tag	M	11	110 ±07	99–122	—	—	—	—	—
2	gummy	L-tag	W-tag	F	1	90 ± –	90–090	—	—	—	—	—
3	gummy	L-tag	G-tag	M	128	108 ±12	79–144	6(0,6,0)	131 ±16	114–145	2224 ±1154	1209–3900
4	gummy	L-tag	G-tag	F	129	112 ±20	77–179	13(0,13,0)	128 ±15	106–152	1698 ±1104	80–3531
5	gummy	S-tag	W-tag	M	32	86 ±28	33–136	—	—	—	—	—
6	gummy	S-tag	W-tag	F	14	65 ±20	38–102	—	—	—	—	—
7	gummy	S-tag	G-tag	M	27	88 ±22	39–119	1(0,1,0)	83 ±–	83–083	52 ± –	52–52
8	gummy	S-tag	G-tag	F	21	63 ±25	32–117	—	—	—	—	—
9	school	J-tag	W-tag	M	59	127 ±26	62–154	18(2,15,1)	146 ±11	125–155	5039 ±4369	705–15251
10	school	J-tag	W-tag	F	41	128 ±33	60–164	14(1,13,0)	152 ±15	113–167	3260 ±2333	319–8380
11	school	L-tag	W-tag	M	32	145 ±07	116–160	7(1,6,0)	155 ±14	143–174	4382 ±3142	841–9539
12	school	L-tag	W-tag	F	15	148 ±15	106–160	4(0,4,0)	161 ±08	155–167	3809 ±5548	546–12114
13	school	L-tag	G-tag	—	4	137 ±18	112–155	2(0,2,0)	152 ±–	152–152	2971 ±0769	2427–3515
14	school	L-tag	G-tag	M	521	141 ±12	71–163	127(4,123,0)	147 ±12	114–175	3858 ±3100	82–15510
15	school	L-tag	G-tag	F	292	137 ±17	73–164	71(6,65,0)	149 ±12	112–167	3142 ±2341	89–9107
16	school	S-tag	W-tag	—	2	67 ±09	60–073	—	—	—	—	—
17	school	S-tag	W-tag	M	14	48 ±06	40–057	2(0,2,0)	83 ±–	83–083	2652 ±2456	915–4389
18	school	S-tag	W-tag	F	14	54 ±06	43–065	5(0,5,0)	107 ±40	57–141	2566 ±1944	260–5262
19	school	S-tag	G-tag	—	15	57 ±12	32–067	2(1,1,0)	—	—	377 ±0434	70–684
20	school	S-tag	G-tag	M	781	54 ±13	31–148	86(7,79,0)	97 ±35	43–159	1568 ±1604	31–7555
21	school	S-tag	G-tag	F	807	53 ±12	31–148	79(13,64,2)	95 ±33	51–159	1221 ±1512	35–6200

Table 2

Description of the second double-tagging experiment for gummy and school sharks. The number of recaptures includes, consecutively and in parentheses, that with two tags, with tag A only, and with tag B only. "—" indicates unknown or not computable; tagging position refers to tag B's position.

Row	Species	Tag A	Tag B	Tagging position	Sex	Number released	Mean length at release (cm)	Length range at release (cm)	Number recaptured	Mean length at recapture (cm)	Length range at recapture (cm)	Mean time at liberty (d)	Range of time at liberty (d)
1	gummy	Jumbo	dart	fin	M	68	115 ±08	97–140	13(9,3,1)	117 ±08	107–130	192 ±119	64–386
2	gummy	Jumbo	dart	fin	F	66	125 ±21	80–176	19(17,1,1)	122 ±10	108–145	119 ±083	13–309
3	gummy	Jumbo	dart	muscle	M	101	109 ±14	87–144	41(22,19,0)	112 ±14	86–148	278 ±232	5–818
4	gummy	Jumbo	dart	muscle	F	164	119 ±21	68–175	43(19,24,0)	123 ±20	91–167	340 ±273	6–1138
5	gummy	Roto	dart	muscle	—	1	106 ± –	106–106	1(0,1,0)	—	—	83 ± –	83–83
6	gummy	Roto	dart	muscle	M	151	96 ±18	45–135	37(20,15,2)	106 ±17	66–148	309 ±262	2–1059
7	gummy	Roto	dart	muscle	F	180	99 ±18	40–136	53(26,26,1)	112 ±14	78–138	278 ±256	1–886
8	school	Jumbo	dart	fin	M	46	135 ±14	108–168	3(3,0,0)	136 ±13	123–149	136 ±089	34–202
9	school	Jumbo	dart	fin	F	81	139 ±12	108–167	15(11,3,1)	141 ±12	110–157	306 ±130	123–546
10	school	Jumbo	dart	muscle	M	77	134 ±11	100–158	12(9,2,1)	140 ±20	107–179	263 ±201	33–633
11	school	Jumbo	dart	muscle	F	53	140 ±14	100–164	9(6,3,0)	142 ±10	122–155	272 ±179	31–551
12	school	Roto	dart	muscle	M	13	108 ±23	71–152	3(3,0,0)	110 ±22	85–124	317 ±164	146–474
13	school	Roto	dart	muscle	F	21	110 ±29	38–160	6(2,4,0)	115 ±15	100–136	229 ±172	34–468

Model

Consider a (single) fish i that is captured, double tagged, and released at time $t_0(i)$. The index i can be used to examine the effects of any factor on the instantaneous tag shedding rate. Let A and B indicate the two types of tags and

$P(i,A,B,t(i))$ = probability of retaining both tags at time $t(i)$;
$P(i,A,0,t(i))$ = probability of retaining only tag A at time $t(i)$;
$P(i,0,B,t(i))$ = probability of retaining only tag B at time $t(i)$;
$P(i,0,0,t(i))$ = probability of retaining neither tag at time $t(i)$;
$\dot{C}(i,A,B,t(i))$ = probability that it is caught at time $t(i)$ and reported given that it has retained both tags;
$\dot{C}(i,A,0,t(i))$ = probability that it is caught at time $t(i)$ and reported given that it has retained only tag A;
$\dot{C}(i,0,B,t(i))$ = probability that it is caught at time $t(i)$ and reported given that it has retained only tag B;
$\dot{C}(i,0,0,t(i))$ = probability that it is caught at time $t(i)$ and reported given that it has retained neither tag;
$\dot{U}(i,A,B,t(i))$ = probability that it is caught at time $t(i)$ but not reported given that it has retained both tags;
$\dot{U}(i,A,0,t(i))$ = probability that it is caught at time $t(i)$ but not reported given that it has retained only tag A;
$\dot{U}(i,0,B,t(i))$ = probability that it is caught at time $t(i)$ but not reported given that it has retained only tag B;
$\dot{U}(i,0,0,t(i))$ = probability that it is caught at time $t(i)$ but not reported given that it has retained neither tag;
$\dot{D}(i,A,B,t(i))$ = probability that it is dead at time $t(i)$ given that it has retained both tags;
$\dot{D}(i,A,0,t(i))$ = probability that it is dead at time $t(i)$ given that it has retained only tag A;
$\dot{D}(i,0,B,t(i))$ = probability that it is dead at time $t(i)$ given that it has retained only tag B;
$\dot{D}(i,0,0,t(i))$ = probability that it is dead at time $t(i)$ given that it has retained neither tag;
$\pi(i)$ = probability that it remains alive after type-I mortality (i.e. mortality due to the immediate effects of tagging and handling);
$\rho(i,j)$ = probability that it retains tag j (j=A,B) after type-I shedding (i.e. tag shedding due to the immediate effects of tagging and handling);
$F(i,t(i))$ = instantaneous rate of fishing mortality at time $t(i)$;
$M(i,t(i))$ = instantaneous rate of natural mortality at time $t(i)$;
$R(i,A,B,t(i))$ = probability of reporting given that it is caught at time $t(i)$ and that it has retained both tags;
$R(i,A,0,t(i))$ = probability of reporting given that it is caught at time $t(i)$ and that it has retained only tag A;
$R(i,0,B,t(i))$ = probability of reporting given that it is caught at time $t(i)$ and that it has retained only tag B;
$R(i,0,0,t(i))$ = probability of reporting given that it is caught at time $t(i)$ and that it has retained neither tag;
$\lambda(i,A,t(i))$ = instantaneous shedding rate of tag A at time $t(i)$; and
$\lambda(i,B,t(i))$ = instantaneous shedding rate of tag B at time $t(i)$.

We assume that, in the time interval $[t(i),t(i)+\Delta t]$, the probability that fish i retaining both tags is caught is $F(i,t(i))\Delta tP(i,A,B,t(i))+O(\Delta t)$, the probability that it is dead is $M(i,t(i))\Delta tP(i,A,B,t(i))+O(\Delta t)$, the probability that it sheds tag A is $\lambda(i,A,t(i))\Delta tP(i,A,B,t(i))+O(\Delta t)$, and the probability that it sheds tag B is $\lambda(i,B,t(i))\Delta tP(i,A,B,t(i))+O(\Delta t)$, where $O(\Delta t)\to 0$ as $\Delta t\to 0$. It is also assumed that these events are independent with no more than one event occurring in the time interval. Under these assumptions, the probability that fish i retains both tags at time $t(i)+\Delta t$ given that it has retained both tags at time $t(i)$ is given by

$$P(i,A,B,t(i)+\Delta t)=[1-F(i,t(i))\Delta t-M(i,t(i))\Delta t-\lambda(i,A,t(i))\Delta t-\lambda(i,B,t(i))\Delta t]\,P(i,A,B,t(i))+O(\Delta t).$$

Taking the limit $\Delta t\to 0$ and letting the dot above a quantity denote the first derivative of that quantity with respect to $t(i)$ yields

$$\dot{P}(i,A,B,t(i))=-[F(i,t(i))+M(i,t(i))+\lambda(i,A,t(i))+\lambda(i,B,t(i))]\,P(i,A,B,t(i)).$$

This and similar arguments yield a tag shedding model of the form

$$\begin{cases} \dot{P}(i,A,B,t(i)) = -\left[F(i,t(i))+M(i,t(i))+\lambda(i,A,t(i))+\lambda(i,B,t(i))\right]P(i,A,B,t(i)) \\ \dot{P}(i,A,0,t(i)) = -\left[F(i,t(i))+M(i,t(i))+\lambda(i,A,t(i))\right]P(i,A,0,t(i))+\lambda(i,B,t(i))P(i,A,B,t(i)) \end{cases} \quad (1)$$

$$
\begin{cases}
\dot{P}(i,0,B,t(i)) = -\left[F(i,t(i)) + M(i,t(i)) + \lambda(i,B,t(i))\right]P(i,0,B,t(i)) + \lambda(i,A,t(i))P(i,A,B,t(i)) \\
\dot{P}(i,0,0,t(i)) = -\left[F(i,t(i)) + M(i,t(i))\right]P(i,0,0,t(i)) + \lambda(i,A,t(i))P(i,A,0,t(i)) + \lambda(i,B,t(i))P(i,0,B,t(i)) \\
\dot{C}(i,A,B,t(i)) = F(i,t(i))R(i,A,B,t(i))P(i,A,B,t(i)) \\
\dot{C}(i,A,0,t(i)) = F(i,t(i))R(i,A,0,t(i))P(i,A,0,t(i)) \\
\dot{C}(i,0,B,t(i)) = F(i,t(i))R(i,0,B,t(i))P(i,0,B,t(i)) \\
\dot{C}(i,0,0,t(i)) = F(i,t(i)) = R(i,0,0,t(i))P(i,0,0,t(i)) \\
\dot{U}(i,A,B,t(i)) = F(i,t(i))\left[1 - R(i,A,B,t(i))\right]P(i,A,B,t(i)) \\
\dot{U}(i,A,0,t(i)) = F(i,t(i))\left[1 - R(i,A,0,t(i))\right]P(i,A,0,t(i)) \\
\dot{U}(i,0,B,t(i)) = F(i,t(i))\left[1 - R(i,0,B,t(i))\right]P(i,0,B,t(i)) \\
\dot{U}(i,0,0,t(i)) = F(i,t(i))\left[1 - R(i,0,0,t(i))\right]P(i,0,0,t(i)) \\
\dot{D}(i,A,B,t(i)) = M(i,t(i))P(i,A,B,t(i)) \\
\dot{D}(i,A,0,t(i)) = M(i,t(i))P(i,A,0,t(i)) \\
\dot{D}(i,0,B,t(i)) = M(i,t(i))P(i,0,B,t(i)) \\
\dot{D}(i,0,0,t(i)) = M(i,t(i))P(i,0,0,t(i))
\end{cases}
\qquad \left[t_0(i) \le t(i)\right] \qquad (1)
$$

continued

with initial conditions

$$
\begin{cases}
P(i,A,B,t_0(i)) = \pi(i)\rho(i,A)\rho(i,B) \\
P(i,A,0,t_0(i)) = \pi(i)\rho(i,A)\left[1 - \rho(i,B)\right] \\
P(i,0,B,t_0(i)) = \pi(i)\left[1 - \rho(i,A)\right]\rho(i,B) \\
P(i,0,0,t_0(i)) = \pi(i)\left[1 - \rho(i,A)\right]\left[1 - \rho(i,B)\right] \\
C(i,A,B,t_0(i)) = 0 \\
C(i,A,0,t_0(i)) = 0 \\
C(i,0,B,t_0(i)) = 0 \\
C(i,0,0,t_0(i)) = 0 \\
U(i,A,B,t_0(i)) = 0 \\
U(i,A,0,t_0(i)) = 0 \\
U(i,0,B,t_0(i)) = 0 \\
U(i,0,0,t_0(i)) = 0 \\
D(i,A,B,t_0(i)) = 0 \\
D(i,A,0,t_0(i)) = 0 \\
D(i,0,B,t_0(i)) = 0 \\
D(i,0,0,t_0(i)) = 0
\end{cases}
$$

Solution of this system of ordinary differential equations as an initial value problem gives

$$
\begin{cases}
P(i,A,B,t(i)) = \pi(i)e^{-\int_{t_0(i)}^{t(i)}[F(i,s)+M(i,s)]ds}\rho(i,A)\rho(i,B)e^{-\int_{t_0(i)}^{t(i)}[\lambda(i,A,s)+\lambda(i,B,s)]ds} \\
P(i,A,0,t(i)) = \pi(i)e^{-\int_{t_0(i)}^{t(i)}[F(i,s)+M(i,s)]ds}\rho(i,A)e^{-\int_{t_0(i)}^{t(i)}\lambda(i,A,s)ds}\left[1-\rho(i,B)e^{-\int_{t_0(i)}^{t(i)}\lambda(i,B,s)ds}\right] \\
P(i,0,B,t(i)) = \pi(i)e^{-\int_{t_0(i)}^{t(i)}[F(i,s)+M(i,s)]ds}\left[1-\rho(i,A)e^{-\int_{t_0(i)}^{t(i)}\lambda(i,A,s)ds}\right]\rho(i,B)e^{-\int_{t_0(i)}^{t(i)}\lambda(i,B,s)ds} \\
P(i,0,0,t(i)) = \pi(i)e^{-\int_{t_0(i)}^{t(i)}[F(i,s)+M(i,s)]ds}\left[1-\rho(i,A)e^{-\int_{t_0(i)}^{t(i)}\lambda(i,A,s)ds}\right]\left[1-\rho(i,B)e^{-\int_{t_0(i)}^{t(i)}\lambda(i,B,s)ds}\right] \\
C(i,A,B,t(i)) = \int_{t_0(i)}^{t(i)}F(i,s)R(i,A,B,s)P(i,A,B,s)ds \\
C(i,A,0,t(i)) = \int_{t_0(i)}^{t(i)}F(i,s)R(i,A,0,s)P(i,A,0,s)ds \\
C(i,0,B,t(i)) = \int_{t_0(i)}^{t(i)}F(i,s)R(i,0,B,s)P(i,0,B,s)ds \\
C(i,0,0,t(i)) = \int_{t_0(i)}^{t(i)}F(i,s)R(i,0,0,s)P(i,0,0,s)ds \\
U(i,A,B,t(i)) = \int_{t_0(i)}^{t(i)}F(i,s)[1-R(i,A,B,s)]P(i,A,B,s)ds \\
U(i,A,0,t(i)) = \int_{t_0(i)}^{t(i)}F(i,s)[1-R(i,A,0,s)]P(i,A,0,s)ds \\
U(i,0,B,t(i)) = \int_{t_0(i)}^{t(i)}F(i,s)[1-R(i,0,B,s)]P(i,0,B,s)ds \\
U(i,0,0,t(i)) = \int_{t_0(i)}^{t(i)}F(i,s)[1-R(i,0,0,s)]P(i,0,0,s)ds \\
D(i,A,B,t(i)) = \int_{t_0(i)}^{t(i)}M(i,s)P(i,A,B,s)ds \\
D(i,A,0,t(i)) = \int_{t_0(i)}^{t(i)}M(i,s)P(i,A,0,s)ds \\
D(i,0,B,t(i)) = \int_{t_0(i)}^{t(i)}M(i,s)P(i,0,B,s)ds \\
D(i,0,0,t(i)) = \int_{t_0(i)}^{t(i)}M(i,s)P(i,0,0,s)ds
\end{cases}
\tag{2}
$$

This tag shedding model follows essentially the same line of thought as Xiao's (1996a) and can be readily phrased in the standard terminology of competing risks in survival analysis (David and Moeschberger, 1978). Also, notice that the left-hand side of Equation 1 sums to zero; the left-hand side of Equation 2 sums to $\pi(i)$.

When a single fish is double tagged and released at time $t_0(i)$, one of 16 mutually exclusive events can happen at time $t(i)$ (Equation 1 or 2). However, only three events are actually observable: the fish has, upon recapture, retained both tags, retained tag A and lost tag B, or lost tag A and retained tag B, with respective probabilities of $\dot{C}(i,A,B,t(i))$, $\dot{C}(i,A,0,t(i))$ and $\dot{C}(i,0,B,t(i))$. The event that it has shed both tags upon recapture, with a probability of $\dot{C}(i,0,0,t(i))$, cannot be observed, for when both tags are shed, a fish cannot be reliably distinguished from one that was never tagged. A likelihood function can be constructed to estimate parameters in Equation 1 or 2 by following arguments in standard competing risk analysis, but these estimates are substantially biased. To overcome this problem, we estimated model parameters by conditioning on observations of three events only, i.e. by maximizing the conditional likelihood function for all reported recaptures with at least one tag retained

$$L=L_1 \cdot L_2 \cdot L_3,$$

with

$$\begin{aligned}
L_1 &= \prod_{h=1}^{n} \frac{\dot{C}(h,A,B,t(h))}{\dot{C}(h,A,B,t(h))+\dot{C}(h,A,0,t,(h))+\dot{C}(h,0,B,t(h))} \\
&= \prod_{h=1}^{n} \frac{R(h,A,B,t(h))\theta(h,A,B,t(h))}{R(h,A,B,t(h))\theta(h,A,B,t(h))+R(h,A,0,t(h))\theta(h,A,0,t(h))+R(h,0,B,t(h))\theta(h,0,B,t(h))} \\
L_2 &= \prod_{j=1}^{m} \frac{\dot{C}(j,A,0,t(j))}{\dot{C}(j,A,B,t(j))+\dot{C}(j,A,0,t(j))+\dot{C}(j,0,B,t(j))} \\
&= \prod_{j=1}^{n} \frac{R(j,A,0,t(j))\theta(j,A,0,t(j))}{R(j,A,B,t,(j))\theta(j,A,B,t(j))+R(j,A,0,t(j))\theta(j,A,0,t(j))+R(j,0,B,t(j))\theta(j,0,B,t(j))} \\
L_3 &= \prod_{k=1}^{p} \frac{\dot{C}(k,0,B,t(k))}{\dot{C}(k,A,B,t(k))+\dot{C}(k,A,0,t(k))+\dot{C}(k,0,B,t(k))} \\
&= \prod_{k=1}^{n} \frac{R(k,0,B,t(k))\theta(k,0,B,t(k))}{R(k,A,B,t(k))\theta(k,A,B,t(k))+R(k,A,0,t(k))\theta(k,A,0,t(k))+R(k,0,B,t(k))\theta(k,0,B,t(k))}
\end{aligned} \tag{3}$$

$$\begin{cases}
\theta(i,A,B,t(i)) = \rho(i,A)\rho(i,B)e^{-\int_{t_0(i)}^{t(i)}[\lambda(i,A,s)+\lambda(i,B,s)]ds} \\
\theta(i,A,0,t(i)) = \rho(i,A)e^{-\int_{t_0(i)}^{t(i)}\lambda(i,A,s)ds}\left[1-\rho(i,B)e^{-\int_{t_0(i)}^{t(i)}\lambda(i,B,s)ds}\right]
\end{cases}$$

$$\begin{cases} \theta(i,0,B,t(i)) = \left[1-\rho(i,A)e^{-\int_{t_0(i)}^{t(i)}\lambda(i,A,s)ds}\right]\rho(i,B)e^{-\int_{t_0(i)}^{t(i)}\lambda(i,B,s)ds} \\ \theta(i,0,0,t(i)) = \left[1-\rho(i,A)e^{-\int_{t_0(i)}^{t(i)}\lambda(i,A,s)ds}\right]\left[1-\rho(i,B)e^{-\int_{t_0(i)}^{t(i)}\lambda(i,B,s)ds}\right], \end{cases} \quad (3)$$

continued

where $h, j,$ and k index fish recaptures with both tags retained, with tag A only, and with tag B only; n, m , and p are the total numbers of fish recaptures with both tags retained, with tag A only, and with tag B only.

In the estimation, we assumed that $t_0(i)=0$, there was no type-I tag shedding (i.e. $\rho(i,A)=\rho(i,B)=1$), and $R(i,A,B,t(i))=R(i,A,0,t(i))=R(i,0,B,t(i))$. The latter assumption makes Equation 3 independent of probability of reporting at time $t(i)$. We also set the instantaneous shedding rate of tag j (j=A,B) as a function of fish total length at release $L(i)$ and time at liberty $t(i)$ of the form $\lambda(i,j,t(i))=\beta_0(j)+\beta_1(j)L(i)+\beta_2(j)t(i)$, where $\beta_0(j)$, $\beta_1(j)$ and $\beta_2(j)$ are parameters to be estimated. Thus, $\lambda(i,j,t(i))$ has three terms and seven (2^3–1) nested models, since each term can be included or excluded in a nested model and a nested model has at least one term. Under these assumptions, Equation 3 becomes

$$L=L_1 \cdot L_2 \cdot L_3, \quad (4)$$

with

$$L_1 = \prod_{h=1}^{n} \frac{\theta(h,A,B,t(h))}{\theta(h,A,B,t(h))+\theta(h,A,0,t(h))+\theta(h,0,B,t(h))}$$

$$L_2 = \prod_{j=1}^{n} \frac{\theta(j,A,0,t(j))}{\theta(j,A,B,t(j))+\theta(j,A,0,t(j))+(\theta(j,0,B,t(j))}$$

$$L_3 = \prod_{k=1}^{n} \frac{\theta(k,0,B,t(k))}{\theta(k,A,B,t(k))+\theta(k,A,0,t(k))+\theta(k,0,B,t(k))}$$

$$\begin{cases} \theta(i,A,B,t(i)) = e^{-[\beta_0(A)+\beta_1(A)L(i)+\beta_0(B)+\beta_1(B)L(i)]t(i)-\frac{1}{2}[\beta_2(A)+\beta_2(B)]t(i)^2} \\ \theta(i,A,0,t(i)) = e^{-[\beta_0(A)+\beta_1(A)L(i)]t(i)-\frac{1}{2}\beta_2(A)t(i)^2}\left[1-e^{-[\beta_0(B)+\beta_1(B)L(i)]t(i)-\frac{1}{2}\beta_2(B)t(i)^2}\right] \\ \theta(i,0,B,t(i)) = \left[1-e^{-[\beta_0(A)+\beta_1(A)L(i)]t(i)-\frac{1}{2}\beta_2(A)t(i)^2}\right]e^{-[\beta_0(B)+\beta_1(B)L(i)]t(i)-\frac{1}{2}\beta_2(B)t(i)^2} \\ \theta(i,0,0,t(i)) = \left[1-e^{-[\beta_0(A)+\beta_1(A)L(i)]t(i)-\frac{1}{2}\beta_2(A)t(i)^2}\right]\left[1-e^{-[\beta_0(B)+\beta_1(B)L(i)]t(i)-\frac{1}{2}\beta_2(B)t(i)^2}\right] \end{cases}$$

For the first experiment, $\lambda(i,A,t(i))=0$ because internal tags (tag A)were inserted into the shark's body cavity and were not shed, except under very unusual circumstances. For the same reason, although three recaptured school sharks appeared to have shed their internal tags (rows 9 and 21, Table 1), these events were actually due to failure to detect the tag upon recapture. Consequently, both tags were assumed to be present for these recaptures. Also, tag shedding rates of white and gray Petersen discs were estimated, singly or in combination, to examine their possible differences (Table 3). Data on $\lambda(i,A,t(i))$(Roto tags)

Table 3

Instantaneous rate of tag shedding for school shark estimated from data based on the first double-tagging experiment assuming that the shedding rates of internal tags (tag A) are zero, i.e., $\lambda(i,A,t(i))=\beta_0(A)=0$, and those of external tags (tag B) depend only on their types, i.e., $\lambda(i,B,t(i))=\beta_0(B)$; n is the number of recaptures. $-\log(L)$ gives values of the negative of the logarithm of the likelihood function; "—" indicates not applicable or not computable. J = J-tag; L = L-tag; S = S-tag; W = W-tag; G = G-tag. The word "and" indicates pooling of data: J and L for pooling data from J-tag and L-tag; M and F for pooling data from males and females. Estimates for tag A of J and L and tag B of G are the same as those for tag A of L and tag B of G; estimates for tag A of J and S and tag B of G are the same as those for tag A of S and tag B of G.

Row	Tag A	Tag B	Sex	n	$\beta_0(B)$ (SE)/yr	$-\log(L)$
1	J	W	M and F	32	0.3718(0.1089)	9.4439
2	J	W	M	18	0.2829(0.1104)	5.4509
3	J	W	F	14	0.5816(0.2946)	3.3332
4	L	W	M and F	11	0.6446(0.3609)	2.3503
5	L	W	M	7	0.3617(0.2605)	1.3295
6	L	W	F	4	—	—
7	L	G	M and F	200	0.7347(0.1012)	45.4817
8	L	G	—	2	—	—
9	L	G	M	127	1.1439(0.2534)	14.3301
10	L	G	F	71	0.5202(0.1016)	27.4639
11	S	W	M and F	7	—	—
12	S	W	—	0	—	—
13	S	W	M	2	—	—
14	S	W	F	5	—	—
15	S	G	M and F	167	3.0653(0.4739)	47.9105
16	S	G	—	2	1.2692(1.5899)	0.3407
17	S	G	M	86	4.5992(1.0705)	18.1029
18	S	G	F	79	2.3509(0.4955)	26.9553
19	L	W and G	M and F	211	0.7291(0.0974)	47.8580
20	L	W and G	—	2	—	—
21	L	W and G	M	134	1.0272(0.2119)	16.8622
22	L	W and G	F	75	0.5466(0.1040)	28.3971
23	S	W and G	M and F	174	3.0857(0.4735)	48.0298
24	S	W and G	—	2	1.2692(1.5899)	0.3407
25	S	W and G	M	88	4.5993(1.0702)	18.1029
26	S	W and G	F	84	2.3912(0.4975)	27.1604
27	J and L	W	M and F	43	0.4165(0.1084)	12.1642
28	J and L	W	M	25	0.2993(0.1016)	6.8258
29	J and L	W	F	18	0.7464(0.3367)	4.0018
30	J and L	W and G	M and F	243	0.6460(0.0780)	59.5387
31	J and L	W and G	—	2	—	—
32	J and L	W and G	M	152	0.7457(0.1255)	27.0143
33	J and L	W and G	F	89	0.5508(0.0979)	31.7369
34	J and S	W	M and F	39	0.4434(0.1207)	11.6709
35	J and S	W	—	0	—	—
36	J and S	W	M	20	0.3162(0.1168)	6.1176
37	J and S	W	F	19	0.7587(0.3557)	4.4422
38	J and S	W and G	M and F	206	1.6579(0.2133)	80.2783
39	J and S	W and G	—	2	1.2692(1.5899)	0.3407
40	J and S	W and G	M	106	1.5043(0.2682)	45.5600
41	J and S	W and G	F	98	1.8729(0.3550)	34.0001

continued

were too limited from the second experiment (Table 2) to estimate two or more parameters. We estimated $\beta_0(A)$ only, which can, however, be scaled to $\beta_1(A)$ or $\beta_2(A)$ given $L(i)$ and $t(i)$. For tag B (Petersen discs or dart tags), all seven nested models of $\lambda(i,B,t(i))$ were fitted, where possible, to data from each tagging experiment. The final and most parsimonious model was decided by the χ^2 statistic (Seber and Wild, 1989, p.196–197). All parameters were estimated by minimizing –log(L) by using the simplex algorithm by a FORTRAN 77 program (available on request).

Results

Maximization of Equation 4 for both sets of tagging data yielded estimates of shedding rate for various (independent) combinations of fish sex, tag type, and tag position, and their (asymptotic) standard errors (Tables 3 and 4). If a tag was retained in all recaptured fish, we assumed that its shedding rate was zero in order to estimate other parameters of the model. Because shedding rates must be nonnegative, the assumption of zero shedding rate will lead to an underestimate of the parameter concerned and introduce a positive bias into the estimates of other parameters. The extent of such bias could be assessed by simulation studies but is beyond the scope of this work.

Fish length at release or time at liberty, or both, entered certain final models for $\lambda(i,B,t(i))$, only when the number of fish recaptured was small. By contrast, whenever there were many fish recaptures (e.g. rows 14–15 and 20–21, Table 1), neither factor entered the final model. Therefore, we conclude that fish length at release or time at liberty, or both, did not significantly affect tag shedding rates; and their inclusion in certain models was a result of too few recaptures.

Fish sex affected tag shedding rates of Petersen discs for some combinations of tag type and tag position. For a combination of a 50-mm-long and 23-mm-wide internal tag (J-tag) with a white Petersen disc (external) tag (W-tag) (rows 1–3, Table 3), $\lambda(i,B,t(i))$=0.3718 (±0.1089)/yr if data are pooled for both sexes of school shark, with a –log-likelihood of 9.4439. For the sex-specific model, $\lambda(i,B,t(i))$=0.2829 (±0.1104)/yr for males; $\lambda(i,B,t(i))$=0.5816 (±0.2946)/yr for females, with a (male and female) combined –log-likelihood of 8.7841 (=5.4509+3.3332). The increase in value of the –log-likelihood function for an extra parameter is, in this case, negligible ($\chi^2_{1,0.2507}$=2×(9.4439–8.7841)=1.3196), suggesting no statistically significant differences in tag shedding rates between sexes for white Petersen discs.

Table 3 (continued)

Row	Tag A	Tag B	Sex	n	$\beta_0(B)$ (SE)/yr	–log(L)
42	L and S	W	M and F	18	0.9094(0.4251)	3.4541
43	L and S	W	—	0	—	—
44	L and S	W	M	9	0.4791(0.3116)	1.7664
45	L and S	W	F	9	—	—
46	L and S	G	M and F	367	1.2892(0.1331)	116.1464
47	L and S	G	—	4	1.2729(1.5769)	0.3409
48	L and S	G	M	213	2.1071(0.3520)	41.2981
49	L and S	G	F	150	0.9537(0.1327)	67.8985
50	L and S	W and G	M and F	385	1.2679(0.1274)	119.8703
51	L and S	W and G	—	4	1.2729(1.5769)	0.3409
52	L and S	W and G	M	222	1.8674(0.2992)	45.8682
53	L and S	W and G	F	159	0.9818(0.1336)	68.9822
54	J and L and S	W	M and F	50	0.4753(0.1168)	14.1985
55	J and L and S	W	—	0	—	—
56	J and L and S	W	M	27	0.3252(0.1063)	7.4610
57	J and L and S	W	F	23	0.8956(0.3763)	4.8981
58	J and L and S	G	M and F	367	1.2892(0.1331)	116.1464
59	J and L and S	G	—	4	1.2729(1.5769)	0.3409
60	J and L and S	G	M	213	2.1071(0.3520)	41.2981
61	J and L and S	G	F	150	0.9537(0.1327)	67.8985
62	J and L and S	W and G	M and F	417	1.0891(0.1026)	137.7412
63	J and L and S	W and G	—	4	1.2729(1.5769)	0.3409
64	J and L and S	W and G	M	240	1.2738(0.1761)	63.3863
65	J and L and S	W and G	F	173	0.9478(0.1251)	72.8067

Table 4

Instantaneous rate of tag shedding for gummy and school sharks estimated from data based on the second double-tagging experiment assuming that $\lambda(i,A,t(i))=\beta_0(A)$ and $\lambda(i,B,t(i))=\beta_0(B)$. Tagging position refers to tag B's position; n is the number of recaptures; $-\log(L)$ gives values of the negative of the logarithm of the likelihood function; "—" indicates not applicable or not computable. The word "and" indicates pooling of data: Jumbo and Roto for pooling data from Jumbo tag and Roto tag; M and F for pooling data from males and females.

Row	Species	Tag A	Tag B	Position of tag	Sex	n	$\beta_0(A)$ (SE)/yr	$\beta_0(B)$ (SE)/yr	$-\log(L)$
1	gummy	Jumbo	dart	fin	M and F	32	0.1912(0.1349)	0.3770(0.1886)	19.5193
2	gummy	Jumbo	dart	fin	M	13	0.2133(0.2125)	0.5642(0.3260)	10.98
3	gummy	Jumbo	dart	fin	F	19	0.1771(0.1770)	0.1890(0.1890)	8.0212
4	gummy	Jumbo	dart	muscle	M and F	84	—	0.9239(-)	67.5957
5	gummy	Jumbo	dart	muscle	M	41	—	0.8550(0.2021)	34.5527
6	gummy	Jumbo	dart	muscle	F	43	—	0.9902(-)	32.9376
7	gummy	Roto	dart	muscle	M and F	91	0.1304(0.0747)	1.0502(0.1712)	71.5838
8	gummy	Roto	dart	muscle	—	1	—	—	—
9	gummy	Roto	dart	muscle	M	37	0.1581(0.1110)	0.8183(0.2187)	31.8327
10	gummy	Roto	dart	muscle	F	53	0.0918(0.0913)	1.2111(0.2563)	37.1817
11	gummy	Jumbo	dart	fin and muscle	M and F	116	0.0569(0.0402)	0.8278(0.1243)	91.8731
12	gummy	Jumbo	dart	fin and muscle	M	54	0.0586(0.0584)	0.8042(0.1749)	47.2285
13	gummy	Jumbo	dart	fin and muscle	F	62	0.0555(0.0553)	0.8503(0.1766)	44.6251
14	gummy	Jumbo and Roto	dart	muscle	M and F	175	0.0641(0.0369)	0.9828(0.1121)	141.3449
15	gummy	Jumbo and Roto	dart	muscle	—	1	—	—	—
16	gummy	Jumbo and Roto	dart	muscle	M	78	0.0809(0.0570)	0.8379(0.1484)	67.8238
17	gummy	Jumbo and Roto	dart	muscle	F	96	0.0447(0.0446)	1.0948(0.1656)	70.9707
18	gummy	Jumbo and Roto	dart	fin and muscle	M and F	207	0.0857(0.0381)	0.9172(0.1012)	164.2892
19	gummy	Jumbo and Roto	dart	fin and muscle	—	1	—	—	—
20	gummy	Jumbo and Roto	dart	fin and muscle	M	91	0.1011(0.0580)	0.8083(0.1361)	79.4274
21	gummy	Jumbo and Roto	dart	fin and muscle	F	115	0.0692(0.0487)	0.9989(0.1474)	82.5257
22	school	Jumbo	dart	fin	M and F	18	0.0973(0.0972)	0.2646(0.1530)	11.0858
23	school	Jumbo	dart	fin	M	3	—	—	—
24	school	Jumbo	dart	fin	F	15	0.1104(0.1103)	0.2948(0.1706)	10.6735
25	school	Jumbo	dart	muscle	M and F	21	0.1041(0.1038)	0.4262(0.1917)	14.7690
26	school	Jumbo	dart	muscle	M	12	0.1727(0.1725)	0.3219(0.2282)	6.6030
27	school	Jumbo	dart	muscle	F	9	—	0.5484(0.3201)	7.3704
28	school	Roto	dart	muscle	M and F	9	—	0.7845(0.3967)	8.5426
29	school	Roto	dart	muscle	M	3	—	—	—
30	school	Roto	dart	muscle	F	6	—	1.6867(0.8865)	5.6360
31	school	Jumbo	dart	fin and muscle	M and F	39	0.1003(0.0708)	0.3466(0.1230)	26.0748
32	school	Jumbo	dart	fin and muscle	M	15	0.1421(0.1419)	0.2700(0.1912)	7.0831
33	school	Jumbo	dart	fin and muscle	F	24	0.0773(0.0772)	0.3831(0.1571)	18.7670
34	school	Jumbo and Roto	dart	muscle	M and F	30	0.0798(0.0796)	0.5339(0.1793)	24.0789
35	school	Jumbo and Roto	dart	muscle	M	15	0.1188(0.1188)	0.2263(0.1602)	7.5881
36	school	Jumbo and Roto	dart	muscle	F	15	—	0.8882(0.3425)	14.0341
37	school	Jumbo and Roto	dart	fin and muscle	M and F	48	0.0876(0.0619)	0.4254(0.1233)	35.8236
38	school	Jumbo and Roto	dart	fin and muscle	M	18	0.1038(0.1037)	0.1997(0.1414)	7.9368
39	school	Jumbo and Roto	dart	fin and muscle	F	30	0.0746(0.0745)	0.5510(0.1755)	26.7306

However, for a combination of a 50-mm-long and 22-mm-wide internal tag (L-tag) with a gray Petersen disc (external) tag (G-tag) (rows 7–10, Table 3), $\lambda(i,B,t(i))$= 0.7347 (±0.1012)/yr if data are pooled for both sexes, with a –log-likelihood of 45.4817. For the sex-specific model, $\lambda(i,B,t(i))$=1.1439 (±0.2534)/yr for males; $\lambda(i,B,t(i))$=0.5202 (±0.1016)/yr for females, with a (male and female) combined –log-likelihood of 41.7940 (=14.3301+27.4639). The increase in value of the –log-likelihood function for an extra parameter is statistically significant ($\chi^2_{1,0.0066}=2\times(45.4817-41.7940)=7.3754$), suggesting significant differences in tag shedding rates between sexes for gray Petersen discs. Similarly, for a combination of a 35-mm-long and 10-mm-wide internal tag (S-tag) with a gray Petersen disc (external) tag (rows 15–18, Table 3), $\lambda(i,B,t(i))$=3.0653 (±0.4739)/yr if data are pooled for both sexes, with a –log-likelihood of 47.9105. For the sex-specific model, $\lambda(i,B,t(i))$=4.5992 (±1.0705)/yr for males; $\lambda(i,B,t(i))$= 2.3509 (±0.4955)/yr for females, with a (male and fe-

male) combined –log-likelihood of 45.0582 (=18.1029+26.9553). The increase in value of the –log-likelihood function for an extra parameter is, again, statistically significant ($\chi^2_{1,0.0169}$=2×(47.9105–45.0582)=5.7046), again suggesting significant differences in tag shedding rates between sexes for gray Petersen discs. Notice, in these cases, that tag shedding rates for males nearly doubled those for females. For the second tagging experiment, no differences in tag shedding rates were found among sexes for either species of shark (Table 4).

The shedding rate of Petersen discs for the school shark was very high. When combined with a 50-mm-long and 23-mm-wide internal tag (J-tag), white Petersen disc (W-tag) had a shedding rate of $\lambda(i,B,t(i))$=0.2829(±0.1104)/yr or $100\times(1-e^{-0.2829}) \approx$ 24.64%/yr for males, and $\lambda(i,B,t(i))$=0.5816(±0.2946)/yr or 44.10%/yr for females (rows 1–3, Table 3). When combined with a 50-mm-long and 22-mm-wide internal tag (L-tag), gray Petersen disc (G-tag) had a shedding rate of $\lambda(i,B,t(i))$=1.1439 (±0.2534)/yr or 68.14%/yr for males and $\lambda(i,B,t(i))$=0.5202 (±0.1016)/yr or 40.56%/yr for females (rows 7–10, Table 3). When combined with a 35-mm-long and 10-mm-wide internal tag (S-tag), gray Petersen disc (G-tag) had a shedding rate of $\lambda(i,B,t(i))$=4.5992 (±1.0705)/yr or 98.99%/yr for males and $\lambda(i,B,t(i))$=2.3509 (±0.4955)/yr or 90.47%/yr for females (rows 15–18, Table 3). Other combinations of tag type and tagging position for the first tagging experiment did not yield reliable (in accuracy and precision) estimates of tag shedding rate because of insufficient data.

For the second tagging experiment, tag shedding rates varied considerably for both species of sharks (rows 1–10 and 22–30, Table 4). However, dart tags had a higher shedding rate than either Roto or Jumbo tags. For example, for male gummy shark tagged in the fin, dart tags had an instantaneous shedding rate of 0.5642 (±0.3260)/yr and Jumbo tags 0.2133 (±0.2125)/yr (row 2, Table 4). For either gummy or school shark, the shedding rate of dart tags placed in the fin was about half that of dart tags placed in the muscle (rows 1–10 and 22–30, Table 4).

Discussion

We developed a simple tag shedding model (Equations 1–4) to account for the effects of time at liberty, sex, size, tag position, and other factors and used a special case to estimate the instantaneous shedding rates of Petersen discs, Roto tags, and dart tags in two species of sharks. It can be used to estimate the shedding rates of two tags, singly or in combination, and has two interesting features. In Equation 1, both $F(i,t(i))$ and $M(i,t(i))$ are independent of the 16 state variables. This independence ensures that $P(i,A,B,t(i))$, $P(i,A,0,t(i))$, $P(i,0,B,t(i))$ and $P(i,0,0,t(i))$ are all expressible as a product (Equation 2), which in turn ensures that terms involving $F(i,t(i))$ and $M(i,t(i))$ in the likelihood function (Equation 3 or 4) are cancelled out. Thus, as in Xiao (1996a), our tag shedding model applies, even when $F(i,t(i))$ and $M(i,t(i))$ are arbitrary functions of time $t(i)$. On the other hand, if fishing and natural mortalities depend on the state variables of tags A and B, then terms in $P(i,A,B,t(i))$, $P(i,A,0,t(i))$, $P(i,0,B,t(i))$ and $P(i,0,0,t(i))$ involving four fishing mortalities $F(i,A,B,t(i))$, $F(i,A,0,t(i))$, $F(i,0,B,t(i))$ and $F(i,0,0,t(i))$ and four natural mortalities $M(i,A,B,t(i))$, $M(i,A,0,t(i))$, $M(i,0,B,t(i))$ and $M(i,0,0,t(i))$ cannot be factored out. Then, for estimation of parameters by maximizing Equation 3, particular functional forms of all the eight mortalities must be hypothesized. This tag shedding model is more general but more data-demanding. The other interesting feature of our tag shedding model is that Equation 3 is independent of probabilities of reporting $R(i,A,B,t(i))$, $R(i,A,0,t(i))$, $R(i,0,B,t(i))$ and $R(i,0,0,t(i))$ if these probabilities are identical, arbitrary functions of time $t(i)$ because of the way they enter Equation 3.

Statistically significant differences in shedding rates of Petersen discs between male and female school sharks were detected when many fish were recaptured. We do not know why such differences existed but we postulate that male sharks have a higher tag shedding rate because they are more active and would tend to rub off the tags and that female sharks have a lower tag shedding rate because they are larger and have thicker fins. An external fin tag, such as a Petersen disc, is shed only after its pin or locking mechanism has cut through the fin. The larger the tagged fish, the thicker is its fin and hence the farther the distance its pin or locking mechanism has to cut through to the posterior edge of the fin. Consequently, larger animals have lower shedding rates. Thus, sex is confounded in its effects with size. That is probably why the length at release of school sharks did not affect the shedding rates of Petersen discs within a wide size range examined, although the loss of anchor tags (Floy tags) was size-dependent for striped bass *Morone saxatilis* (Waldman et al., 1990) but size-independent for lake trout *Salvelinus namaycush* (Fabrizio et al., 1996). We could not detect differences between sexes with fewer recaptures, however, because the use of Equation 1 or 2 to resolve sexual differences in tag shedding rate requires many recaptures (see below).

Shedding rates of Petersen discs, Roto tags, and dart tags did not change with time at liberty. Some

tagged fish have higher shedding rates than others, because tags that are less securely attached are shed earlier. The proportion of less securely attached tags decreases with increasing time at liberty. This will yield an apparent decrease in tag shedding rate with time at liberty. A similar argument applies when tag shedding rates vary among individuals. The lack of a trend may indicate negligible tag losses from improper attachment, insignificant individual variability in tag shedding rate, or insufficient data (see below).

Estimates of tag shedding rates in Tables 3 and 4 must be used cautiously because only those that are based on many recaptures are reliable, whereas those that are based on few recaptures are unreliable. For example, the estimates of tag shedding rates for a combination of a 50-mm-long and 22-mm-wide internal tag (L-tag) with a white Petersen disc (W-tag, external) (rows 4–6, Table 3) were based on only 11 recaptures (rows 11 and 12, Table 1), only one of which had retained both tags (row 11, Table 1), and hence are unreliable. No estimates could even be obtained for a combination of a 35-mm-long and 10-mm-wide (S-tag) internal tag with a white Petersen disc (W-tag, external) (rows 11–14, Table 3), despite seven recaptures, none of which had retained both tags (rows 16–18, Table 1). Similarly, no estimates could be obtained, for any tag combinations, from data on gummy sharks from the first double-tagging experiment, despite 20 recaptures, none of which had retained both tags (rows 1–8, Table 1). Equally unreliable estimates of tag shedding rates could also result from pooling of information while ignoring differences in its sources. For example, estimates from pooling all three internal tags (i.e. J-tag, L-tag and S-tag) (rows 54–65, Table 3) should be treated cautiously because of sexual differences inferred above. By contrast, for both sexes of school sharks, the estimates of shedding rates of gray Petersen discs are reliable for its combination with a 50-mm-long and 22-mm-wide internal tag (L-tag) (rows 9 and 10, Table 3) or with a 35-mm-long and 10-mm-wide (S-tag) internal tag (rows 17 and 18, Table 3) because information from many fish recaptures was used in their estimation. Much less reliable estimates were obtained for dart tags on gummy sharks (rows 5, 6, 9, and 10, Table 4). Although rather high in all cases, all these shedding rates are actually underestimated, as will be shown and published elsewhere.

Although we have examined only the effects of tag type, sex, length at release, and time at liberty on tag shedding, many other factors, such as tagging operator (Hampton, 1996), can also affect tag shedding rate. However, hundreds or even thousands of fish need to be recaptured (many more need to be released) to estimate effects of tagging operators reliably. Such a great demand of data is well expected of Equation 1 or 2, which is a compartmental model. The solution of a compartmental model can be given by a linear combination of exponentials and is known to yield bad ill-conditioning (Seber and Wild, 1989, p. 118–119). Indeed, for some compartmental models, no amount of data is sufficient for identifying model parameters. Similarly, the "best" model of all possible models of a general model is identifiable only by a sufficient volume of data. As mentioned above, fish length at release or time at liberty, or both, entered certain "best" models for $\lambda(i,B,t(i))$, when the number of fish recaptured was small, but did not, when there were many fish recaptures. This finding suggests that fewer data than sufficient cannot identify the "best" model. To detect and address problems with parameter and model identifiability for a particular general model (e.g. Equation 1 or 2), one might generate as large a set of data as necessary, for example, by duplicating each record of an existing set of data from a double-tagging experiment a necessary number of times, analyse it, and design one's tagging experiment accordingly (e.g. to determine the number of fish to be released and the expected number of fish to be recaptured).

Results of our study have major implications for future double-tagging experiments for estimating instantaneous tag shedding rate and for analysis of tagging data. Because estimation of a single parameter requires many fish recaptures and hence incurs considerable financial resources, use of an easily detected and permanent tag eliminates a need for considering tag loss and is preferred in any tagging experiment. However, with a commercially or recreationally harvested species, problems of tag reporting remain. Use of two readily detectable, identical tags with a moderate shedding rate in a double-tagging experiment reduces the number of parameters to be estimated by one half. A moderate shedding rate is necessary because too low a shedding rate requires some recaptures after a long time at liberty for reliable estimation of parameters; too high a shedding rate renders the tag useless for some applications.

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Areas, depths, and times of high discard rates of scup, *Stenotomus chrysops*, during demersal fish trawling off the northeastern United States

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In the waters off the northeastern United States, many stocks of commercial and recreational species have declined in recent years (Anthony, 1993; Sissenwine and Rosenberg, 1994; Collins, 1995; Matthiessen, 1995; NEFSC, 1995). Although much of the blame for these declines is ascribed to sustained overfishing, there also has been substantial concern over bycatch and discarding practices in key fisheries of the region, especially those involving demersal trawling (Murawski, 1994; Howell and Langan, 1987, 1992; Cadrin et al., 1995; Kennelly et al., 1997).

For many years scup (or porgy, *Stenotomus chrysops*) has been an important commercial species in the mid-Atlantic and southern New England regions, caught principally by otter trawling and to a lesser extent by pound nets, floating trap nets, and fish traps (Shepherd and Terceiro, 1994). Like many other key species in the region, annual commercial landings of this species have declined markedly in recent years from between 18,000 and 27,000 metric tons (t) in the 1950s and 60s to 6000 t in 1992 and 4400 t in 1993 (NEFSC, 1995). There is also an important recreational fishery for scup in this region, and recreational landings in recent years have accounted for 20 to 50% of the total annual catch. These have also declined from an estimated 3,100 t in the 1980s to 2100 t in 1992 and 1300 t in 1993 (NEFSC, 1995). Scientists at the 1995 Northeast Regional Stock Assessment Workshop for the scup stock in this region concluded that 1) it is currently overexploited; 2) it is at a low level of biomass; and 3) current high rates of exploitation of age 0–2 fish should be decreased as much as possible (NEFSC[1]).

As predicted by Wilk and Brown (1980) some time ago, one of the causes of mortality for young scup in this region is thought to be the incidental bycatch and subsequent discarding of this species from demersal trawlers that target other species, particularly squid (*Loligo* spp.). McKiernan and Pierce's[2] study of the inshore squid fishery in Nantucket and Vineyard Sounds, Massachusetts, showed significant discard of scup but, like Cadrin et al. (1995), they concluded that the inshore abundances of this species were more probably related to trawl effort throughout the region than to the relatively small effort of inshore squid trawlers. They concluded that significant numbers of small scup may be discarded by squid trawlers farther offshore where scup are known to migrate in the autumn (see also Finkelstein, 1971; Eklund and Targett, 1990) and recommended an examination of the discarding practices of these trawlers.

The most reliable way to quantify discards in commercial fisheries is for observers to record data during normal fishing operations (e.g. Jean, 1963; Powles, 1969; Young and Romero, 1979; Atkinson, 1984; Murawski et al., 1995). Information from such programs is a necessary prerequisite for the two main management alternatives used to reduce discards: 1) spatial and temporal closures to fishing in areas and times of high rates of discard of key species (i.e. discard "hotspots") (Murawski, 1992; Hendrickson and Griffin, 1993; Alverson et al., 1994, Kennelly, 1997); and 2) modifications to fishing gears and practices that improve selectivity (Robertson and Stewart, 1988; Isaksen et al., 1992; Hall, 1994; Broadhurst et al., 1996; Broadhurst and Kennelly, 1997).

Since 1989, the National Marine Fisheries Service's Northeast Fisheries Science Center (NEFSC) has operated a large-scale observer program in many of the fisheries off the northeastern United States from Maine to North Carolina (Murawski et al., 1995; Kennelly et al., 1997). The data collected from demersal trawlers in this program have provided an opportunity to examine the spatial and temporal occurrences of discarded scup in the offshore mid-Atlantic and southern New England trawl fishery.

[1] NEFSC (Northeast Fisheries Science Center). 1995. Report of the 19th northeast regional stock assessment workshop–the plenary. NOAA/NMFS/NEFSC, Woods Hole, MA. NEFSC Ref Doc. 95-09, 57 p.

[2] McKiernan, D. J., and D. E. Pierce. 1995. *Loligo* squid fishery in Nantucket and Vineyard Sounds. Massachusetts Div. Fish. Publ. 17648-75-200-1/95-3.47-CR, 62 p.

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Materials and methods

Field sampling

Each month between July 1990 and June 1994, Manomet Center for Conservation Sciences (under contract to the NEFSC) placed observers on board demersal trawlers working throughout the northeastern United States. The selection of vessels and trips undertaken did not adhere to any consistent survey design but was based on changing national, management and stock assessment priorities (Murawski et al., 1995) in addition to varying concentrations of fishing fleets in particular areas and times. As a consequence, the observer coverage of these trawlers was highly uneven throughout the period; some areas and times received high sampling and others received very little or no sampling. Of relevance to this paper are the observer data gathered in the southern New England and mid-Atlantic areas shown in Figure 1.

During observed trips, the contents of the codend from each tow were emptied onto the deck and sorted by the crew. If the entire catch could not be sampled, data were collected from a representative subsample. The data collected from each tow that were of relevance to this paper were the following: area, depth, date, time and tow duration, the weights of retained and discarded individuals of various species in the catch, the number of species caught, and the total weights of all species retained or discarded. Because of various operational and logistic reasons, not all tows from all trips were sampled for the weights of retained and discarded species; however, the data examined in this paper include only those tows that were completely sampled.

Analysis of data

Because of the lack of a consistent survey design in this observer program, the data generated could not be regarded as randomly collected, independent samples of the trawling effort of the region, and thus violated the basic assumptions required for conventional statistical analyses (see also Kennelly et al., 1997). Nevertheless, because of the size of the data set and its extensive spatial and temporal coverage, large subsets of data could be extracted for many areas and months and therefore permitted the identification of certain key areas, depths, and times of consistently high rates of scup discard (see "Results" section). The first and broadest examination of the data was to plot the discard rates for scup for all the areas sampled in the region to identify those areas that experienced consistently high rates. Next, discard rates for scup from each sampled tow in each of these identified areas was plotted against depth to

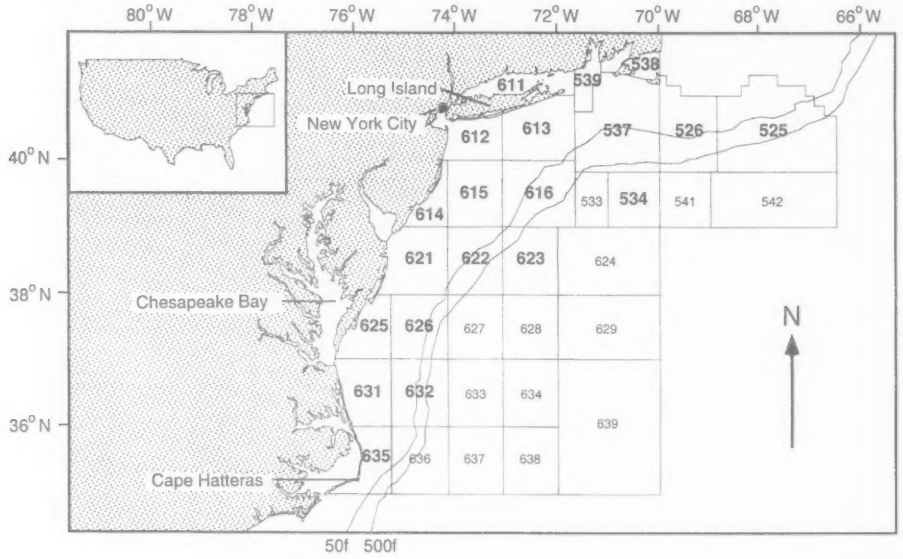

Figure 1

Map showing the various NMFS statistical areas examined in the present paper. Areas labelled in bold are those with sufficient observer coverage to be examined in Figure 2.

determine which depths yielded consistently high rates. Once these depths were identified, the discard rates of scup in these tows were plotted against time to determine the particular months when the high discards occurred. In this way, the large observer data set for the region was focussed to identify the particular areas, depths, and months that yielded high discard rates for scup. Finally, catches of other common species in these identified areas and times were examined by plotting their retention and discard rates.

Results

Figure 2 shows the average discard rates for scup (in pounds per hour towed) for the areas defined in Figure 1. All areas other than 526, 537, 539, 613, 615, 616, 621, 622, and 623 showed low discard rates for scup (defined as a maximum rate of less than 20 lb/h) or low levels of observer coverage (defined as less than 10 observed tows during the study), or both.

Figure 3 shows discard rates for scup against the depth of the tows sampled in each of the areas identified in Figure 2 above. Most areas recorded high discard rates across a range of depths, except areas 613 and 621 which showed marked concentrations from 30–40 fathoms (fm) and 6–17 fm respectively.

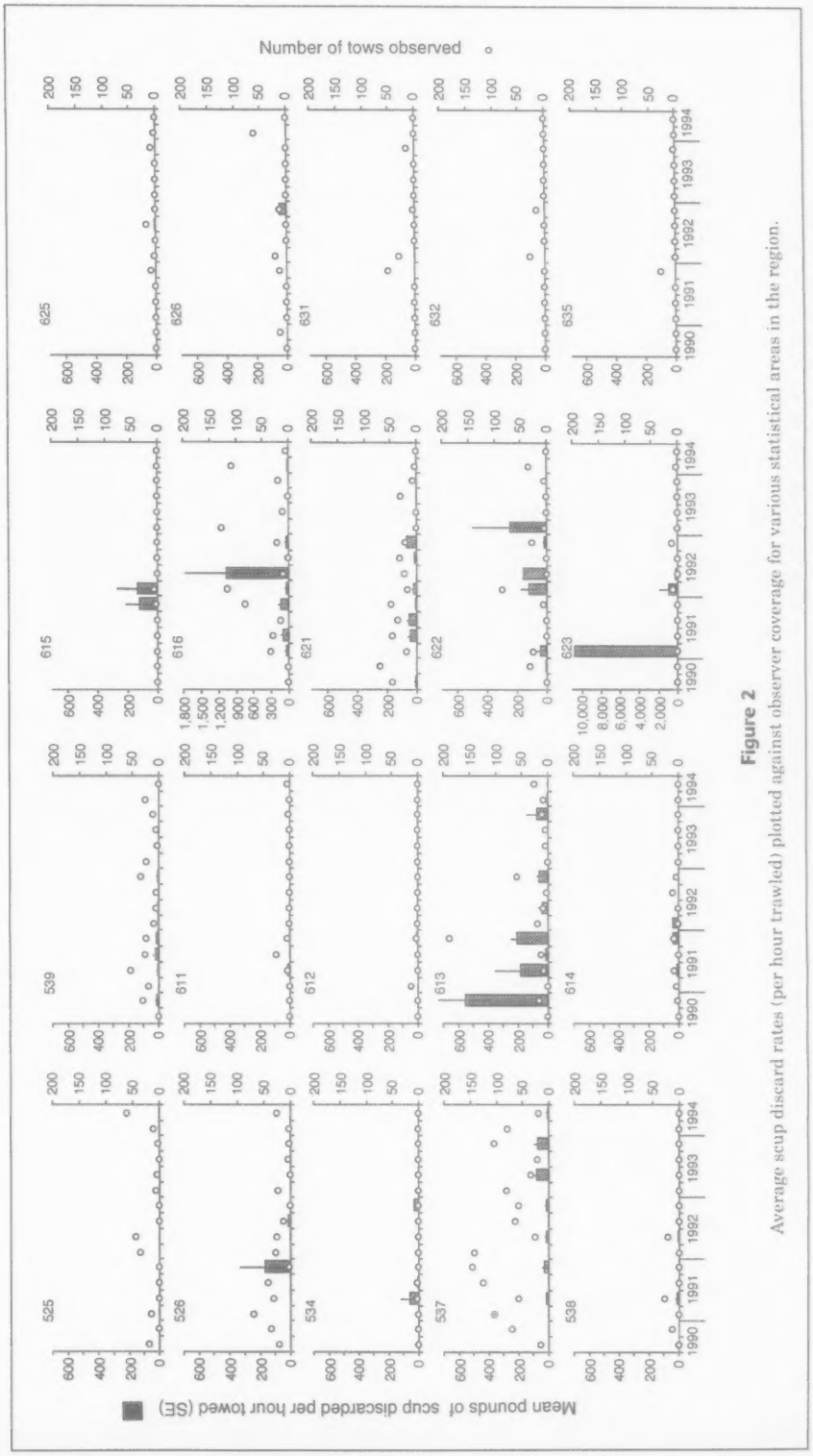

Figure 2

Average scup discard rates (per hour trawled) plotted against observer coverage for various statistical areas in the region.

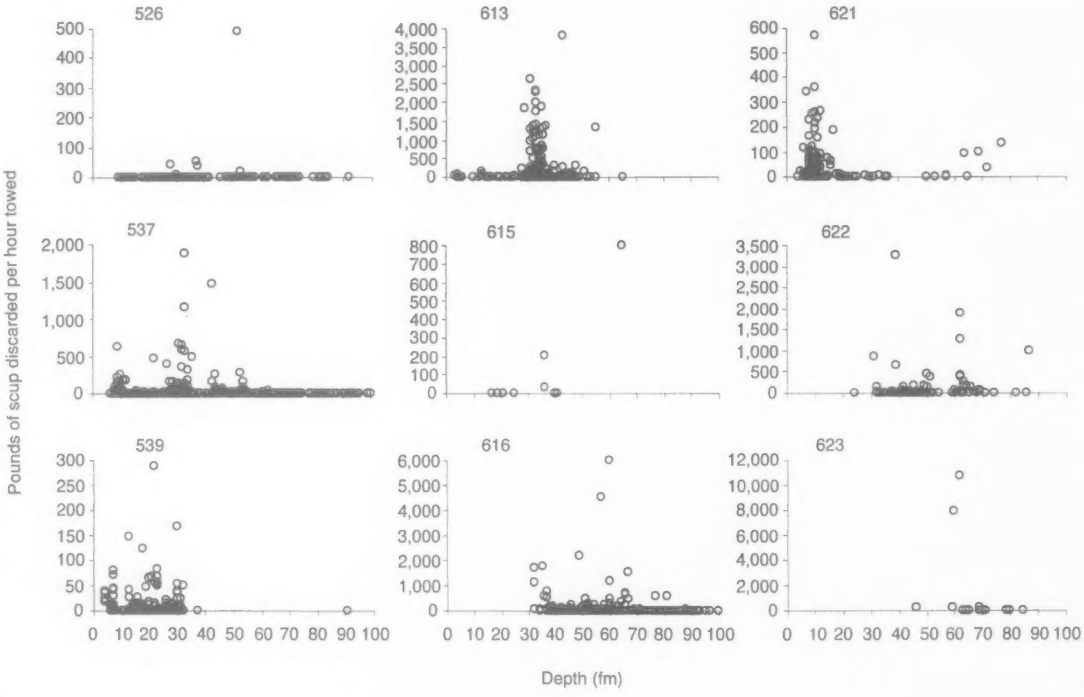

Figure 3

Scup discard rates (per hour trawled) plotted against depth for those areas in Figure 2 that showed consistently high rates of scup discard.

Figure 4 shows the timing of discard rates for scup in area 613 between 30 and 40 fm and in area 621 between 6 and 17 fm. For area 613, the highest rates at those depths occurred in November and December of each of the four years studied. Such a persistent trend for high scup discards was not evident for area 621, where highest rates occurred in May, August, and September 1991, and in September and October 1992.

Figure 5 shows the mean number of pounds retained and discarded for the most common species caught in all tows sampled in area 613, between 30 and 40 fm, in the months of November and December each year. Because of inconsistent identifications, data for squid and skates include data for all such species. Squid were by far the main retained species with an average of 507 lb/h. Scup and whiting, *Merluccius bilinearis,* were also retained in significant quantities at 227 and 223 lb/h respectively. The main discarded species was dogfish, *Squalus acanthias,* (672 lb/h), followed by scup (319 lb/h) and skates (236 lb/h), and lesser quantities of butterfish, *Peprilus triacanthus,* (96 lb/h), whiting (72 lb/h), and red hake, *Urophycis chuss,* (51 lb/h).

Discussion

The above treatment of a four-year subset of the NMFS sea sampling database indicated that trawling in a particular area (area 613), depth (30–40 fm), and time of year (November to December), consistently led to high discard rates for scup. Before discussing this result, however, it is necessary to consider the problems inherent in the data analyzed. In particular, the design of this observer program involved a nonrandom, nonindependent allocation of sampling effort that was uneven in space and time (see Fig. 2). These problems precluded 1) the use of conventional statistical analyses to detect trends and 2) the identification of patterns for all areas for all months. For example, the uneven observer coverage may have resulted in the identification of only 9 of the 20 statistical areas in the region as having high discard rates for scup (Fig. 2). Although adequate observer coverage seemed to occur across most of the depths in many of these nine areas (Fig. 3), not all areas had all depths sampled, precluding the conclusion that other depth-related areas of high scup

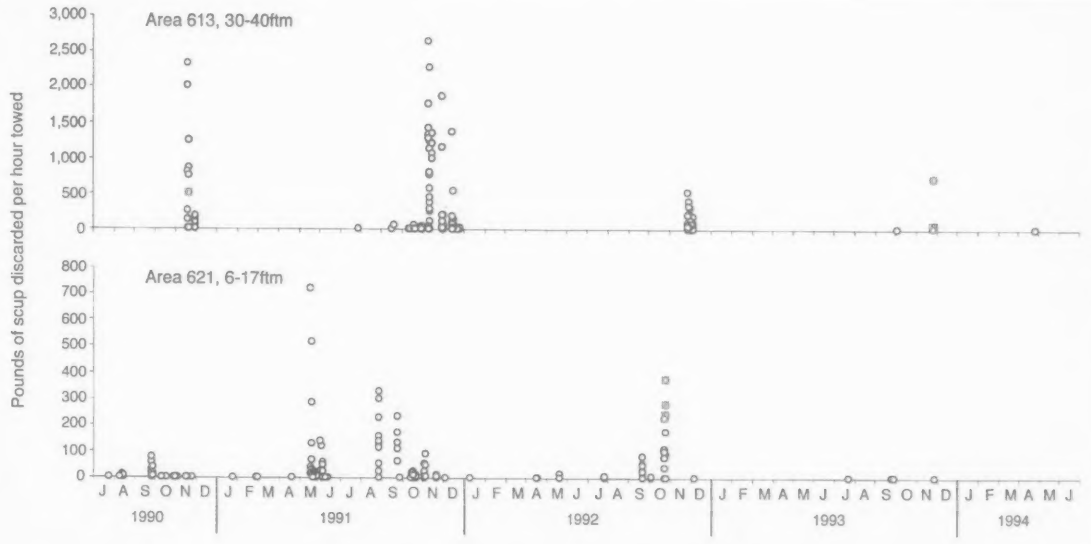

Figure 4

Scup discard rates (per hour trawled) plotted against time for those depths and areas in Figure 3 that showed consistently high rates for scup discard.

discard did not exist in the region (i.e. in addition to the identified depths in areas 613 and 621). Figure 4 shows the temporal pattern of scup discard in those areas and depths identified from Figures 2 and 3 and reveals a consistent pattern of high discard for area 613 but not for area 621. However, more observer coverage throughout the year could have provided evidence of other consistent peaks of scup discard in one or more areas and depths, or could have defined better the small period of high scup discard in area 613. For example, the data indicated that November and December were key months, but more sampling in October and January could have widened this time frame.

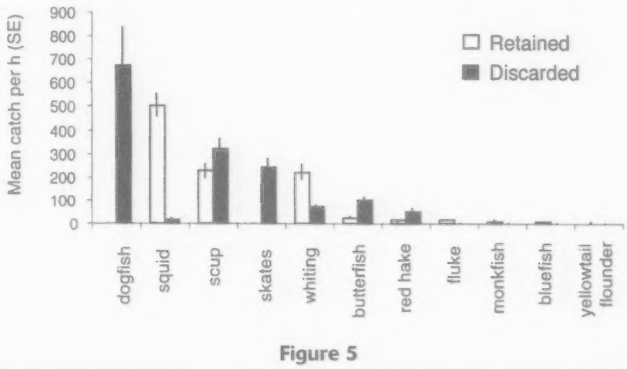

Figure 5

Retained and discard rates (per hour trawled) of the main species caught in those tows done in area 613, between 30 and 40 fm, in the months of November and December (the identified area and time of consistently high rates for scup discard).

A second problem with the data is that they were collected from many different boats, with different nets, horse powers, tow durations, etc. Although such problems are avoided in fishery-independent surveys by using standardized gears and sampling protocols, they are unavoidable when dealing with observer programs whose objective is to survey normal fishing operations across a variety of vessels, gear-types, etc. in order to detect fleet-wide patterns. Variation in observer data is inherent in all such programs, and it is only by doing properly designed and replicated, stratified, randomized observer surveys that such problems can be accounted for.

In most studies that have quantified bycatches, species-specific spatial, and temporal variabilities in

discarding often preclude the identification of definite areas and times of persistently high discards of species (see also Robin, 1991; Martinez et al., 1993; Liggins and Kennelly, 1996; Kennelly et al., 1997). The present study shows that high discard rates for scup were rarely consistent in particular areas and times, although one area and time did show some persistence throughout the four years: the relatively small area (area 613) off Long Island, New York, between 30 and 40 fm in the months of November and December each year. It is well known that from May to August each year scup spawn in estuaries, bays, and inshore areas south of Cape Cod (e.g. see Wilk and Brown, 1980; Eklund and Targett, 1990), particularly around Long Island (Finkelstein, 1971). In autumn, after spawning, they migrate south at greater depths towards their wintering grounds from southern New Jersey to Cape Hatteras, returning back to their inshore spawning grounds in spring (see Neville and Talbot, 1964; Wilk and Brown, 1980; Jeffries and Terceiro, 1985; Eklund and Targett, 1990). It is apparent from this behavior, that the occurrence of large numbers of scup as trawl discards in area 613 off Long Island in the autumn of each year coincides with their migration from Long Island's inshore waters to their wintering grounds farther south.

When spatial and temporal patterns in observer data reveal persistent areas and times of high discard rates, they can be used by fisheries managers to identify where and when various management tools can be applied to reduce discards. These tools usually involve either spatial or temporal closures to fishing (or both) or modifications to fishing gears and practices that reduce discards.

If fisheries managers consider the area and time of high scup discard identified in this paper as a candidate for a closure, the data in Figure 5 provide some information on the consequences this may have on landings of squid and other species. In the identified area and time, an average of over 507 lb of squid were retained per hour towed, whereas an average 319 lb of scup were discarded per hour towed. The actual numbers of fish involved were not available but, because the discarded scup were those individuals considered too small to retain, discarded weights often represent more individual fish per pound than retained weights. One could expect, therefore, that closing this area at this time would protect significant numbers of small scup, thereby assisting the 1995 Northeast Regional Stock Assessment Workshop's recommendation to decrease their exploitation (NEFSC[1]). Larger quantities of dogfish and lesser quantities of skates, butterfish, and whiting would also be protected by such a closure. The "cost" of such a closure, however, would be significant reductions in the landings of squid from the area at that time and lesser reductions in the landings of scup and whiting. One way of estimating the potential effects that such a closure strategy might have for the region is to compare the overall squid retained and scup discard rates with rates adjusted by excluding all tows done in the identified area and time. Throughout the region, the overall discard rate for scup during the four years was 37.5 lb/h (standard error (SE)=4.7), but if the tows done in the identified area and time are excluded, the overall rate falls to 27.3 lb/h (SE=4.5): a decrease of 27%. This should be compared to the overall retained rate of squid in the region of 128.5 lb/h (SE=6.1) falling to 114.9 lb/h (SE=6.0) if the tows done in the identified area and time are excluded —a decrease of 10.6%. It is important to note, however, that closing the area at this time to trawling will not simply remove trawling effort from the region but merely redirect it to other areas that may yield lower scup discards. This means that the effects on landings and discards in the region will not simply be those protected inside the closure but will be tempered by increased landings and discards outside the closure by the redirected vessels.

The other suite of management tools available to reduce discards in areas and at times of high discarding involve modifying fishing gears and practices to improve selectivity. Such modifications as the Nordmore Grid and square-mesh panels have proven successful in reducing discards of small fish in trawl fisheries (e.g. Carr, 1989; Isaksen et al., 1992; Broadhurst et al., 1996; Broadhurst and Kennelly, 1997), and modifications like downward sorting grids and horizontal panels in nets have reduced the bycatches of unwanted sizes of species in groundfish trawls (see Larsen and Isaksen, 1993; Engas and West[3]). For the issue of scup discarding in the northeastern United States, gear modifications would be a better management alternative than the closure strategy outlined above if they could reduce greater quantities of scup discards (and concomitantly reduce landings of squid and other species by smaller amounts) than those under a closure strategy. Such a general, gear-based solution is also advantageous because its adoption throughout the region would not only lead to reductions in scup discard in identified "hotspots" but in all areas where scup discarding occurs. The information provided in the present study identifies the ideal locations and times for any gear-based research that aims to reduce scup discard by trawlers and where and when any gear modifications

[3] Engas, A., and C. W. West. 1995. Development of a species-selective trawl for demersal gadoid fisheries. Int. Coun. Explor. Sea Council Meeting (CM) 1995/B+G+H+J+K:1.

should be initially implemented. At the time of writing this paper, several such gear-based discard reduction programs are currently underway in the region.

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Effects of live-bait shrimp trawling on seagrass beds and fish bycatch in Tampa Bay, Florida

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The use of live shrimp for bait in recreational fishing has resulted in a controversial fishery for shrimp in Florida. In this fishery, night collections are conducted over seagrass beds with roller beam trawls to capture live shrimp, primarily pink shrimp, *Penaeus duorarum*. These shrimp are culled from the catch on sorting tables and placed in onboard aerated "live" wells. Beds of turtlegrass, *Thalassia testudinum*, a species that has highest growth rates and biomass during summer and lowest during the winter (Fonseca et al., 1996) are predominant areas for live-bait shrimp trawling (Tabb and Kenny, 1969). Because of their use in seagrass beds, roller trawls were designed to roll over the bottom to reduce gear penetration and debris collection. Because turtlegrass has an extensive root system, it is not likely to be uprooted by roller trawls, but the roller on the trawl has been noted to break off and collect old turtlegrass leaves (Woodburn et al. 1957). On the Gulf Coast of Florida, bait shrimp are generally collected from turtlegrass beds year-round, but most shrimp are taken October through February (Berkeley et al., 1985). Trawl and culling times for this fishery, including that of Tampa Bay, are typically short, 5–20 and 2–15 min, respectively, to reduce debris collection and both injury and mortality to shrimp. Although no data were collected, Berkeley et al. (1985) suggested that such trawling for shrimp may be destructive to seagrass beds and juvenile fishes, including spotted seatrout, *Cynoscion nebulosus*, snapper, *Lutjanus* spp., and pigfish, *Orthopristis chrysoptera*. However, the effects of this type of trawling on finfish bycatch mortality are unknown.

Numerous studies of fish bycatch mortality have used otter trawls. These include consideration of the effects otter trawling has on cod, *Gadus morhua*, and American plaice, *Hippoglossoides platessoides*, in the Gulf of St. Lawrence, Canada (Jean, 1963); on red snapper, *Lutjanus campechanus*, in the Gulf of Mexico (Gutherz and Pellegrin, 1988); and on bycatch in the Torres Strait, Australia (Wassenberg and Hill, 1989; Harris and Poiner, 1990; Hill and Wassenberg, 1990). In these studies fish mortality ranged from 10% (Jean, 1963) to 80% (Jean, 1963; Wassenberg and Hill, 1989), depending on culling times, animal size, and temperature. Trawl and culling times (30–60 minutes and 15–45 minutes, respectively) in these studies were typically longer than those used by the Florida live-bait shrimp fishery.

Our study objectives were 1) to determine effects of a roller beam trawl on turtlegrass biomass and morphometrics during intensive (up to 18 trawls over a turtlegrass bed), short-term (3-hour duration) use and 2) to examine the mortality of bycatch finfish following capture by a trawl.

Methods

Sampling was done in August and November 1990 in Tampa Bay, Florida (Fig. 1). A commercial bait shrimp boat towed two 3.38 m wide, 0.8 m high stainless steel roller beam trawls simultaneously, one

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from each side of the vessel. These consisted of a net attached to a stainless steel frame with a slotted roller along the entire lower portion of the frame. Stainless steel finger bars, 0.8 m long, were fastened vertically, 5 cm apart, along the front top of the frame to exclude seagrass and other debris (Berkeley et al., 1985). Each roller beam trawl weighed ~75 kg. Nets were constructed of 2.56-cm stretched mesh and had a 1.90-cm stretched mesh tail bag.

Turtlegrass

Nine trawl areas were selected in turtlegrass beds near Tarpon Key (Fig. 1). Each consisted of a marked 40-m × 3.38-m plot of continuous turtlegrass cover. Within each 40-m plot, a central 20-m × 3.38-m impact area was marked. During August, we sampled turtlegrass by removing cores of it within the impact area of each plot prior to trawling and after 1, 3, and 9 trawls. In November, new plots were marked and samples were collected prior to trawling and again after 9 and 18 trawls. Trawl levels were increased in November because preliminary analysis of the August data did not reveal a significant effect on turtlegrass at the maximum trawl level.

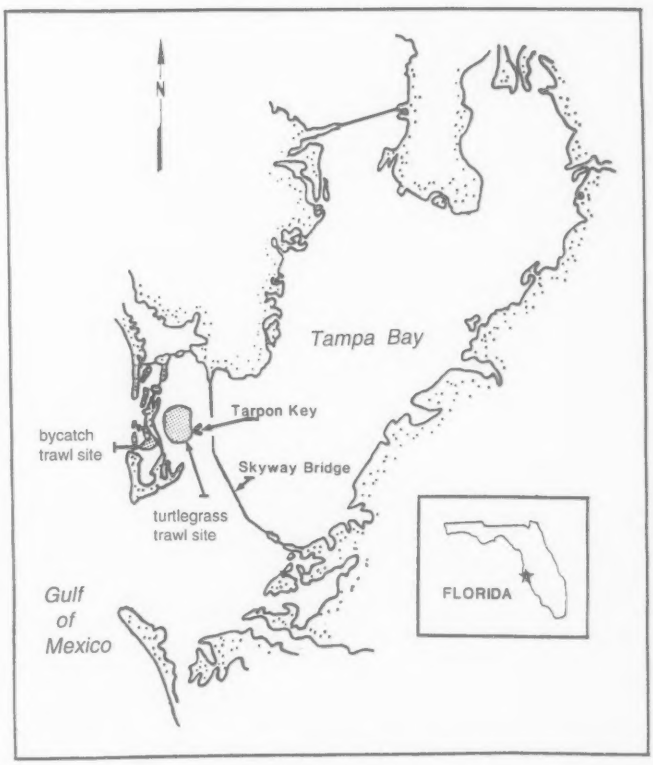

Figure 1

Location of bycatch and turtlegrass trawl sites within Tampa Bay, Florida, 27°40' North latitude, 82°27' West longitude.

Five 15-cm diameter × 20-cm deep substrate cores were taken randomly along a lengthwise midline transect within each impact area at each specified trawl level. For each core the shoot density, longest blade length, total blade length per shoot, and number of blades per shoot (from three randomly selected shoots) were recorded. The turtlegrass standing crop for each core was measured separately for above- and below-ground dry-weight biomass (dried at 60°C for at least 48 hours).

The sequential seagrass measurements within each replicate plot were used in regression analysis to detect rates of decrease for each of the different plant parameters as a function of trawl level. The regression slope (rate of decrease) for each plot was calculated for each plant parameter. Mean rate of decrease for each plant parameter was calculated for each month (all plots combined, n=9 for each month). T-tests were used to compare differences (P<0.05) in mean rate of decrease for each plant parameter for each month.

Mortality of bycatch fish

The bycatch collection site was southwest of Tierra Verde, near the mouth of Tampa Bay (Fig. 1). Each month 30 trawls of 5-min duration were made at this site over three consecutive nights. Trawl and culling times selected were based on observations of commercial live-bait shrimp fishing vessels and shortest times observed used to obtain conservative estimates of bycatch fish mortality. In August, the catch from one net of a trawl pair was allowed to sit on the culling table for 2 min prior to placement in the on-deck live well. The catch from the other trawl net was discarded. While the catch was sitting on the culling table, algae and detritus were removed to reduce subsequent fish entanglement. To reduce the effect of predation on mortality estimates, hardhead catfish, *Arius felis*, were removed from the catch. Bycatch for each trawl was placed in its own separate holding pen, which was held on deck inside an aerated 300-L live well until transferred to a final unvegetated holding site. Holding pens along with bycatch contents were transferred from the on-deck live well to the holding site in a 76-L seawater tank. On-deck holding times were 15 min, transport 5 min. Once at the holding site, pens were placed in the water at a low tide depth >1 m (the minimum) and anchored.

Holding pens were cubical, 1.25 m on each side, constructed of 6.4-mm mesh and had removable mesh tops. A 5-cm diameter polyvinylchloride collar was attached around the top sides of the pen to provide floatation. The mesh top and float collar prevented fish from escaping over the sides, and the top prevented avian predation. Lead-core line was sewn to the bottom seams of each pen to maintain pen volume. Loops attached to each corner of the pen enabled us to anchor the pens with conduit poles.

Owing to low abundance of fish bycatch in November, collection methods were modified; the bycatch from both of the paired trawl nets was combined (only a single trawl net was processed in August), and placed into a single holding pen. Handling procedures were also changed to estimate fish bycatch mortality more conservatively by eliminating catch culling time. In November the catch was placed directly into an aerated 76-L transport tank and during transport to the hold site, algae, detritus, and hardhead catfish were removed. Thus, bycatch mortality results for the two months were not directly comparable. In addition, during November the holding pens were deployed prior to bycatch collection, and the trawl catch was subsequently transferred from the 76-L transport tank into individual holding pens.

Pens were checked for dead fish (no opercular movement) following initial placement at the hold site, and then at intervals of 2, 8, 12, 24, and 36 hours. Checks involved inspecting each holding pen by systematically lifting portions of the pen netting so that the entire volume, net sides, and bottom could be visually inspected for dead fish while allowing surviving fish to remain immersed. Dead fish were collected at each time check and preserved in 10% formalin. At 36 hours, all dead and live fish were separated and preserved. Fish were identified, and standard length and body depth were measured (to the nearest 0.5 mm). The number of individuals and weights of each species (to the nearest 0.01 g) were recorded for each trawl and holding pen time check. Fish with a body depth <7.5 mm were excluded from survival measurements because they were able to escape through the mesh and would cause an unrepresentative mortality estimate.

Because the number of individuals per species per trawl was generally <5, we pooled all 30 trawls for each month to assess survival. The more numerous fish species (spotted seatrout, *Cynoscion nebulosus*, pinfish, *Lagodon rhomboides*, and silver perch, *Bairdiella chrysoura)* were subdivided into small (25.0–65.0 mm standard length, SL) and large (65.5–125.0 mm SL) size classes for mortality comparisons. Mojarra, *Eucinostomus* spp. (including silver jenny, *Eucinostomus gula*), were smaller and were subdivided into small (25.0–55.0 mm) and large (55.5–95.0 mm) size classes so that we could examine size-related mortality. Determination of differential size-class mortality was tested with log-linear model analysis ($P<0.05$).

Salinity and air and water temperatures were measured hourly during bycatch trawling.

Results

Turtlegrass

Regression analysis to estimate mean rate of decrease showed no significant ($P>0.05$) reduction in mean shoot density, number of blades per shoot, longest blade length per shoot, total blade length per shoot, or above- and below-ground biomass with increased trawling during either month. Monthly vegetation measurements at each trawl level (all nine sites combined) are shown in Table 1.

Fish bycatch

We collected a total of 5901 fish representing 42 species; 3262 fish (29 species) in August, 2639 fish (36 species) in November. Mojarra (including silver jenny) were 79.3% (August) and 52.1% (November) of the total catch (Table 2). Most mojarra were smaller than 40 mm SL and were identified as *Eucinostomus* spp., whereas all larger Gerreidae could be identified as silver jenny. The unreliability of the identification of smaller Gerreidae (those smaller than 40 mm SL) precluded their definitive identification to species (Matheson and McEachran, 1984). Mojarra less than 40 mm composed 60.0% (August) and 24.7% (November) of all fish collected, and silver jenny represented 19.3% (August) and 27.4% (November) of all fish collected (Table 2).

Survival was variable (0–100%) among species and months (Table 2; Fig. 2). Among the abundant species (those with at least 20 individuals for each month), high survival was observed for gulf toadfish, *Opsanus beta*, pigfish, pinfish, and gray snapper, (Table 2; Fig. 2). Abundant species with low survival were silver perch, mojarra, silver jenny, and spotted seatrout. Greatest mortality in most species occurred within the first 8 or 12 hours after collection (Fig. 2).

Small fish were significantly ($P<0.05$) more susceptible to trawl-induced mortality than larger fish (Table 3). This was particularly evident for silver perch, spotted seatrout, pinfish, and mojarra (including silver jenny).

Species-specific survival was greater in November than August (Table 2; Fig. 2). For those species for which at least 20 individuals were collected each

month, an average increase of 30.5% species-specific survival was observed in November compared with August. Silver perch (63.6%), gulf pipefish, *Syngnathus scovelli*, (48.1%), and gray snapper (35.0%) had the highest survival increases.

Average air and water temperatures observed were 31 and 32°C, respectively, in August, 23 and 24°C, respectively, in November. Salinity averaged 35 ppt during both months.

Discussion

Because roller trawls were designed to reduce seagrass fragment collection, it has been assumed that they have minimal impact on seagrass habitat (Tabb and Kenny, 1969; Berkeley et al., 1985). We were unable to detect significant trawl impacts on shoot density, structure, or biomass of turtlegrass by intensive short-term (18 trawls within three hours) trawling. This finding supports conjectures by Woodburn et al. (1957) and Tabb and Kenny (1969) that roller trawls have minimal impact on turtlegrass habitat.

However, we did not test for effects of repetitive trawling over turtlegrass beds over a longer period of time. Trawling may cause elevated localized turbidity, which could chronically reduce the potential for seagrass to perform photosynthesis (Kenworthy and Haunert, 1991). In contrast, limited trawling in areas with substantial epiphytic growth and numerous senescent turtlegrass leaves may enhance light availability by removing old plant parts (Woodburn

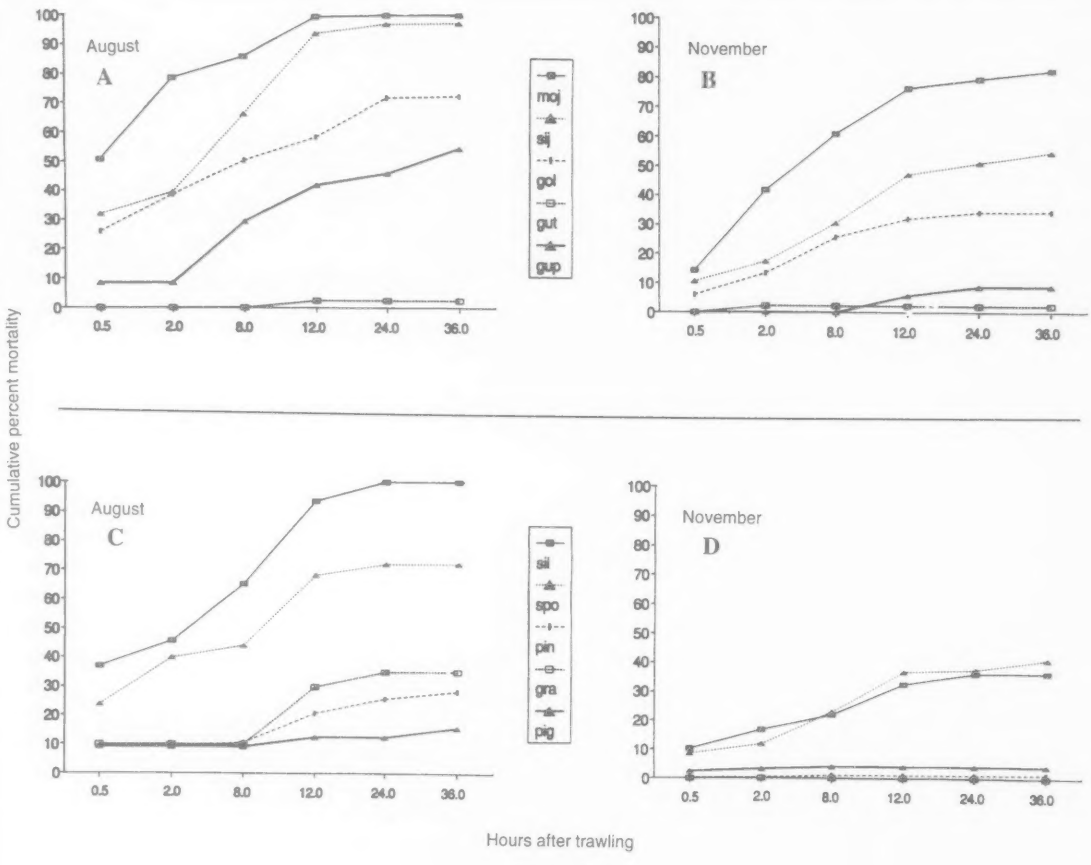

Figure 2

(**A–D**) Cumulative percent mortality in August and November of the abundant (at least 20 individuals per sample month) species collected with shrimp trawls and held in floating pens for 36 h. As noted in the text, handling procedures differed between the two collection periods. Species codes: moj = mojarra, sij = silver jenny, gol = goldspotted killifish, gut = gulf toadfish, gup = gulf pipefish, sil = silver perch, spo = spotted seatrout, pin = pinfish, gra = gray snapper, and pig = pigfish.

et al., 1957) and epiphytic growth from the plants (author's personal observation).

Trawling may affect associated faunal communities by collecting and redistributing macroalgae and turtlegrass litter. Redistribution can reduce the habitat complexity of one area and increase that of another. The alteration of habitat can in turn influence species composition and abundance (Gore et al., 1981; Kulczycki et al., 1981; Leber, 1985).

Fish species were not equally susceptible to mortality by exposure or net injury. Regardless of handling procedures, mojarra were highly susceptible to mortality. At the other extreme, oyster toadfish and striped burrfish, *Chilomycterus schoepfi*, were much less susceptible to trawl-induced mortality. Because of differential species mortality, fish species diversity and composition may be altered in areas of intense or long-term trawling.

Mortality and size were inversely related for numerous species, also noted by Jean (1963) for cod and American plaice, and by Fritz and Johnson (1987) for freshwater drum, *Aplodinotus grunniens*. A pos-

Table 1

Mean (±1 SE) shoot density, morphometrics, and biomass of turtlegrass per 176.7 cm^2 at selected trawl levels during August and November. For each trawl level during a month $n = 9$.

Number of trawls	Shoot density	Number of blades per shoot	Longest blade per shoot (cm)	Total length all blades per shoot (cm)	Above-ground biomass (g)	Below-ground biomass (g)
August						
0	8.1 (0.8)	2.5 (0.1)	31.6 (3.0)	63.5 (7.4)	1.3 (0.1)	7.4 (0.6)
1	7.1 (1.1)	2.4 (0.1)	32.4 (2.0)	61.3 (3.7)	2.3 (0.4)	7.0 (1.1)
3	7.8 (0.9)	2.4 (0.1)	34.0 (2.6)	64.4 (6.4)	2.2 (0.2)	7.2 (1.0)
9	9.1 (0.9)	2.4 (0.1)	28.3 (1.6)	55.2 (3.3)	1.5 (0.1)	8.3 (0.8)
November						
0	10.2 (0.7)	2.3 (0.1)	24.1 (1.2)	41.4 (2.7)	1.1 (0.1)	7.1 (0.6)
9	10.4 (0.4)	2.3 (0.1)	23.7 (0.9)	40.2 (2.0)	1.2 (0.1)	7.5 (0.5)
18	10.4 (0.6)	2.2 (0.1)	23.3 (1.4)	38.3 (2.3)	1.1 (0.1)	7.3 (0.6)

Table 2

Fish collected during August and November live-bait shrimp trawling in Tampa Bay, Florida. Percent survival was determined 36 hours after collection.

		Total number caught		Percent of total catch		Percent survival	
Common name	Scientific name	August	November	August	November	August	November
Mojarra (<40 mm)	*Eucinostomus* spp.	1956	655	60.0	24.7	0.5	18.2
Silver jenny	*Eucinostomus gula*	629	725	19.3	27.4	3.2	45.7
Goldspotted killifish	*Floridichthys carpio*	182	82	5.6	3.1	36.8	65.0
Pinfish	*Lagodon rhomboides*	152	259	4.7	9.8	71.7	98.1
Scaled sardine	*Harengula jaguana*	52	11	1.6	0.4	15.8	54.6
Silver perch	*Bairdiella chrysoura*	46	77	1.4	2.9	0.0	63.6
Rainwater killifish	*Lucania parva*	42	9	1.3	0.3	28.6	44.4
Gulf toadfish	*Opsanus beta*	40	101	1.2	3.8	97.5	98.0
Pigfish	*Orthopristis chrysoptera*	32	122	1.0	4.6	84.4	95.9
Spotted seatrout	*Cynoscion nebulosus*	25	117	0.8	4.4	28.0	59.0
Gulf pipefish	*Syngnathus scovelli*	22	33	0.7	1.2	45.8	93.9
Gray snapper	*Lutjanus griseus*	20	46	0.6	1.7	65.0	100.0
Striped burrfish	*Chilomycterus schoepfi*	13	198	0.4	7.5	100.0	99.5
Blackcheek tonguefish	*Symphurus plagiusa*	11	21	0.3	0.8	63.6	90.5
Planehead filefish	*Monacanthus hispidus*	1	84	<0.1	3.2	0.0	95.2
Southern puffer	*Sphoeroides nephelus*	0	26	0.0	1.0		96.2
Others		39	73	1.2	2.8	33.3	82.2

sible explanation for perceived differences in trawl-induced mortality between small and large size-class fish may be attributed to larger fish having a greater proportion of muscle tissue and larger energy stores than smaller fish; the larger fish are thus able to avoid net contact during prolonged trawl tows, (Fritz and Johnson, 1987). This may cause small fish to be more susceptible than large fish to stress and mortality due to capture. Consequently, high mortality of small individuals, directly or indirectly due to trawling, could potentially reduce the local stock of juvenile fish. This reduction in juvenile fish in turn could reduce the reproductive potential of a species and alter species diversity and composition within affected areas (Wassenberg and Hill, 1989).

Greater survival during November was most evident for silver perch, gulf pipefish, and gray snapper. However, we were not able to assess whether observed increased survival was the result of changes in handling procedures that we instituted (culling versus no culling), or to seasonal factors, such as differences in water temperature as noted by Jean (1963), between our survey months. The 2-min culling time and high August air temperature may have substantially stressed the fish in our study. Also, the higher water temperature in August may have reduced the ability of fish to recuperate from handling because of increased respiratory demand (Alderdice, 1963; Bond, 1979) and lower ambient dissolved oxygen levels (Raymont, 1980). However, even with the changes in handling instituted in November to reduce stress, net injury alone appeared to cause substantial mortality in mojarra, spotted seatrout, silver perch, and goldspotted killifish, *Floridichthys carpio*. Mean size of fish caught was larger in November than in August; this too may have contributed to the higher survival observed.

Table 3

Percent fish mortality in relation to standard length (mm) for species with 20 or more individuals collected during each month. Parentheses indicate number of individuals in a size class. Asterisks (*) indicate significant differences $P<0.05$), based on log-linear model analysis, in mortality between size classes.

Species	Collection period	Size class (mm)	
		25.0–65.0	65.5–125.0
Silver perch	August	100.0 (42)	100.0 (4)
	November*	46.0 (50)	14.8 (27)
Spotted seatrout	August*	65.0 (20)	20.0 (5)
	November*	52.6 (78)	17.9 (39)
Pinfish	August*	47.1 (34)	22.9 (118)
	November		1.5 (259)
		25.0–55.0	55.5–95.0
Mojarra	August	99.1 (2435)	92.2 (153)
	November*	71.0 (1256)	28.0 (125)

Fish abundance per holding pen was not recorded until the end of the 36-h mortality observation period. Because of this, and the fact that predation of live and dead individuals within the pens was not measured, the mortality for smaller species or smaller individuals of a species may be conservative. However, the initial confinement may have also enhanced the survival of injured or disoriented fish by reducing predation that might have been experienced in an open system. Even if bycatch organisms survive trawling and culling they may be quite susceptible to predation. High postrelease predation on bycatch has been observed by prawn trawlers (Hill and Wassenberg, 1990), and this fate probably awaits much of the bycatch overboarded during bait-shrimp trawling. Many bait-shrimp boat captains have reported schools of hardhead catfish following boats and feeding on the bycatch as it is thrown overboard. We similarly observed numerous hardhead catfish and other predatory fish following our boats and feeding on bycatch, and numerous such predatory individuals were collected during our sampling.

Trawl-induced mortality may occur past our 36-h observation period. Numerous fish still alive after the 36-h observation period had missing caudal fins or ulcers, or both. Such fish are were susceptible to subsequent mortality through predation or infection, or both. Moreover, individuals recaptured and culled again in heavily exploited areas could suffer high mortality rates because of cumulative stress. To understand better the effects of this fishery on the resident fauna, we need additional evaluation of the effects of temperature on mortality; the consequences of postrelease predation, delayed mortality due to initial sublethal damage, and subsequent infection; and finally an evaluation of the potential for recapture of bycatch fish.

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Distribution and relative abundance of sea turtles caught incidentally by the U.S. pelagic longline fleet in the western North Atlantic Ocean, 1992–1995

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The distribution and abundance of threatened and endangered species of sea turtles in offshore waters are not well understood. Early oceanographic flights designed to record sea surface temperatures along the Atlantic continental shelf by the U.S. Coast Guard illustrated that aerial surveys for large pelagic fish, marine mammals, and sea turtles were possible (Deaver[1]). Aerial surveys have since proven a cost-effective method of obtaining observational data on sea turtles and have helped researchers understand basic distributional patterns (Hoffman and Fritts, 1982; Fritts et al., 1983; Schroeder and Thompson, 1987; Shoop and Kenney, 1992). Additional sources of pelagic sea turtle data are fishery observer and vessel logbook programs. The U.S. Atlantic pelagic longline fishery for tuna, *Thunnus* spp., and swordfish, *Xiphias gladius*, incidentally captures threatened and endangered sea turtles, which have either ingested baited hooks or become entangled or hooked externally, or both. This paper examines the seasonal distribution and relative abundance of these turtles caught incidentally by the U.S. Atlantic pelagic longline fleet from 1992 through 1995.

Materials and methods

The fishery data used in this analysis are from the National Marine Fisheries Service (NMFS) pelagic logbook program managed by the Southeast Fisheries Science Center, Miami Laboratory. The logbook program was initiated in 1991 and requires U.S. Atlantic longline vessels to report daily catch and effort data. Specific longline information from the pelagic logbooks includes target species, type of bait, set and haulback dates and positions, length of mainline, number and lengths of gangions and floatlines, and numbers of light sticks and hooks set (Cramer, 1996). Sea turtle bycatch information was added to the logbook data form in 1992. Only sets targeting tuna or swordfish, or both, are analyzed here because the shark longline fishery is significantly different temporally, spatially, and geographically. NMFS logbook data for 1992–95 were analyzed by nine geographic fishing areas established by the NMFS Miami Laboratory (Fig. 1). Biological data of captured turtles were provided by NMFS observers placed aboard selected longline vessels (Lee et al., 1995; Gerrior, 1996). Sea turtle species identifications from the logbook data were edited to include only leatherback, *Dermochelys coriacea*, and loggerhead, *Caretta caretta*, sea turtles. This decision was based on the known distribution, abundance, and biology of sea turtles in the area, and the fact that some vessel captains and NMFS observers were unable to identify accurately all turtles encountered.

Results and discussion

The typical U.S. pelagic tuna and swordfish longline consists of a mainline, suspended horizontally by floats at a set depth, that has a series of baited hooks hanging vertically. The gears used for both target species are essentially the same. However, swordfish fishermen generally work at night using chemical light sticks suspended above the hooks to attract bait fish and tuna fishermen generally fish during the day without light sticks. Still, there are indications from logbook data that some of the longline fleet apparently target both tunas and swordfish and alter fishing strategies and gear configurations depending on the main target species, geographic location, and season (Hoey, 1983; Sakagawa et al., 1987). The U.S. pelagic longline fishery has evolved over the years from cumbersome New England style gears to lighter Florida style gears (Berkeley et al., 1981) and are significantly different from the gears used by the Japanese who targeted bluefin tuna in the western Atlantic (Lopez et al., 1979; Witzell, 1984). The gears currently in use on U.S. vessels vary considerably; they average about 47 km long and have 429 hooks suspended by 174 floats 54 m below the sur-

[1] Deaver, J. W. 1975. Aerial oceanographic observations, July 1969–June 1970, Cape Cod, Massachusetts to Miami, Florida. U.S. Dep. Trans., Coast Guard Oceanogr. Unit, Oceanogr. Rep. CG 373-68, 27 p. [NTIS Accession No. AD-A014 415.]

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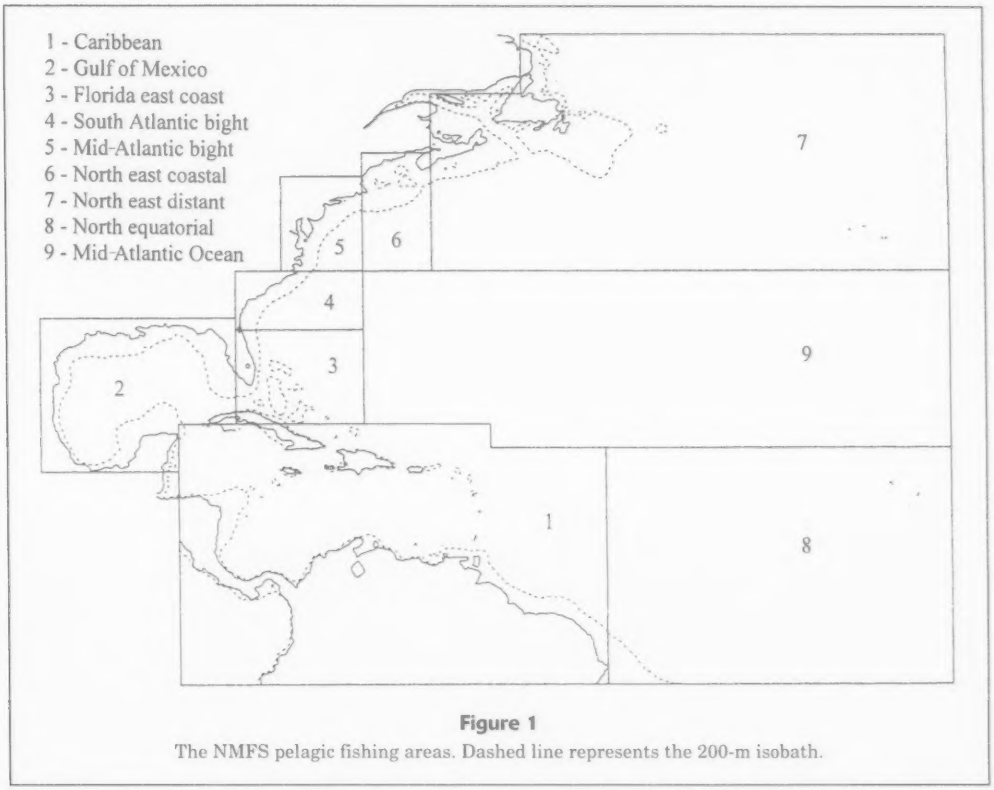


Figure 1
The NMFS pelagic fishing areas. Dashed line represents the 200-m isobath.

face (Power[2]). Pelagic longline fishing effort also changes temporally and spatially, depending on target species, season, and location (Fig. 2), although the overall effort for the entire area has not changed significantly over recent years (Cramer, 1996). Most effort is closely associated near the 200-m isobath along the edge of the continental shelf off the U.S. and off the shelf near the southeastern edge of the Grand Banks and often coincides with major current systems and thermally dynamic areas (Podesta et al., 1993). The most noticeable seasonal shift in fishing effort is the summer–fall swordfish fishery at the Grand Banks that moves to the Caribbean in the winter.

Leatherback sea turtles

A total of 1264 leatherback sea turtle captures were recorded in the NMFS pelagic logbooks for 1992–95 (Table 1). Total numbers of individual turtles caught are unknown because some turtles may have become entangled more than once. Year-round leatherback captures averaged 316 individuals per year (range: 198–452); June through November were the most important months with 1047 captures (82.7%). The mid-Atlantic, northeast coast, and northeast distant waters (areas 5–7) were the most productive, with 1035 (81.9%) combined captures. Of these, the northeast distant (area 7) accounted for 593 (46.8%) of the total leatherback turtle captures. Leatherback sea turtles are captured sporadically throughout the fishing area in the winter and spring seasons and become more abundant during the summer and fall, particularly in fishing areas 5–7 (Fig. 3). September was the most productive month with 278 (21.9%) captures for these areas combined. Reported catches varied annually (Table 2). Leatherback sea turtles were too large for observers to bring on deck for length and weight measurements, but the mean estimated carapace length of 110 individuals observed from the decks of northwest Atlantic fishing vessels was 160 cm.

Catch-per-unit-of-effort (CPUE) values indicated that loggerhead sea turtle capture rates varied considerably between areas (Table 3) but were highest

[2] Power, J. H. 1995. Analysis of the longline fishery effort, catch, and bycatch in the southwest Atlantic and Gulf of Mexico. U.S. Dep. Commer., Natl. Mar. Fish. Serv. Southeast Regional Office, 9721 Executive Center Drive, North, St. Petersburg, FL 33702. NOAA-NMFS-MARFIN Final Report, NA37FF0040-01, 96 p.

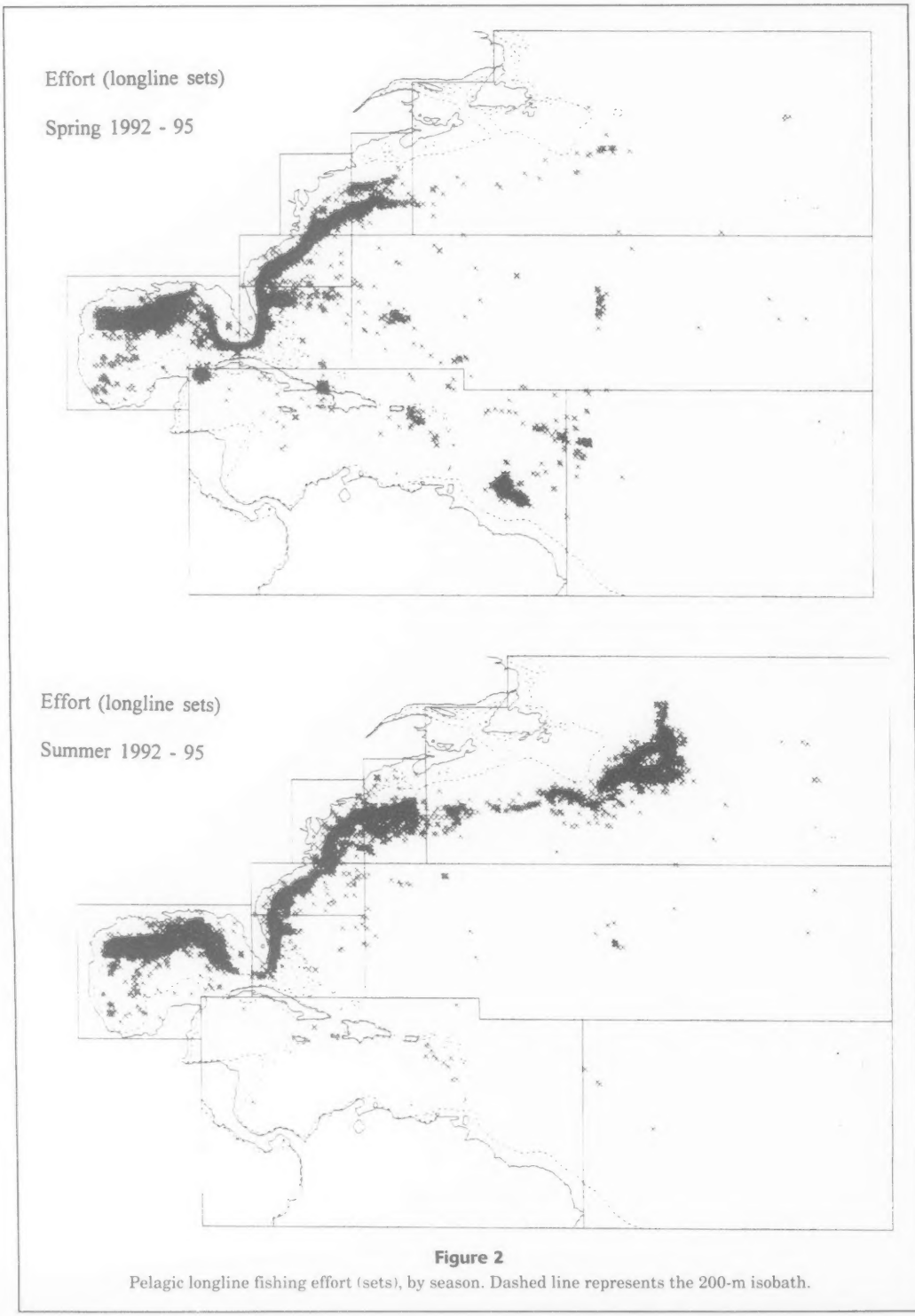


Figure 2

Pelagic longline fishing effort (sets), by season. Dashed line represents the 200-m isobath.

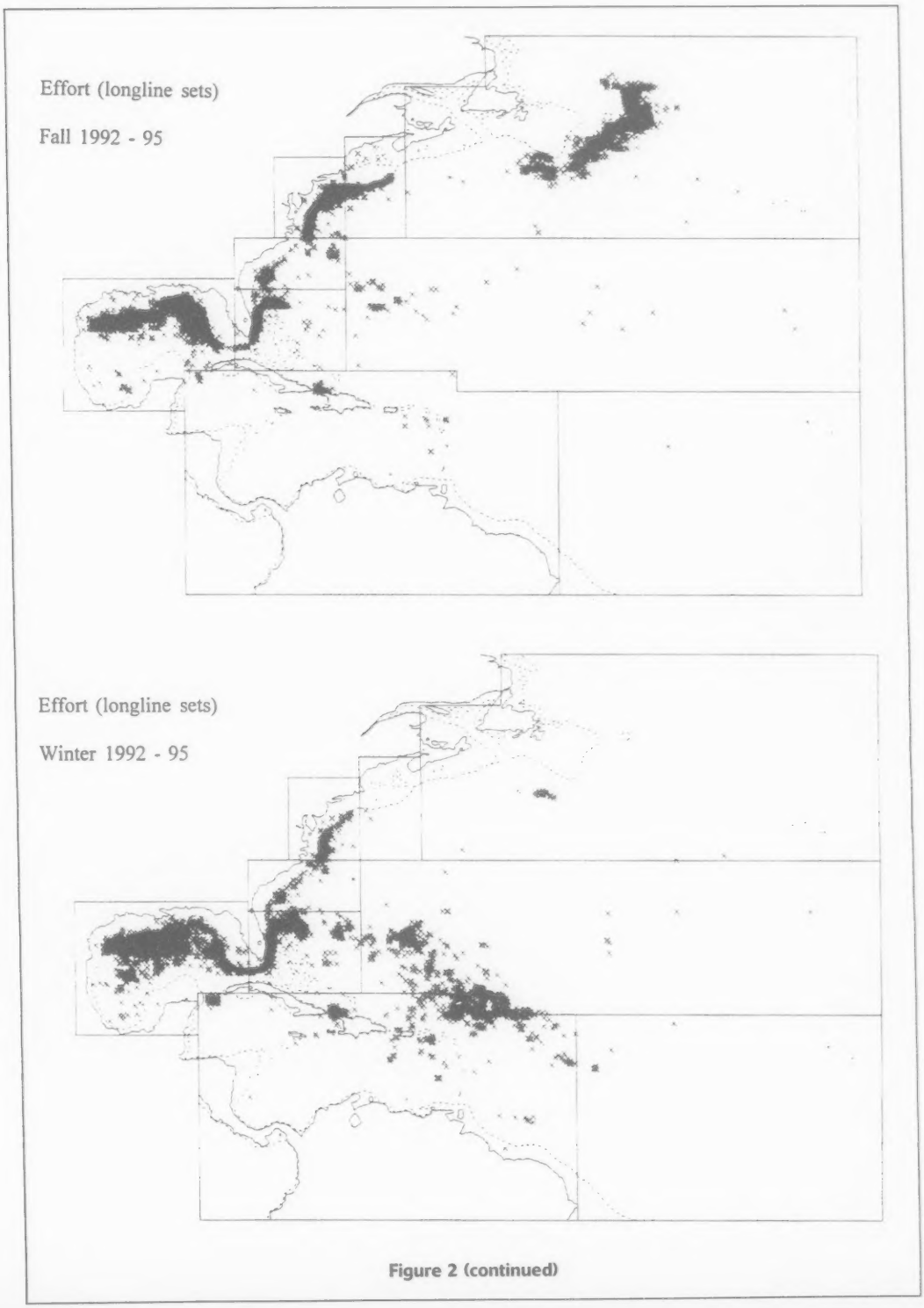


Figure 2 (continued)

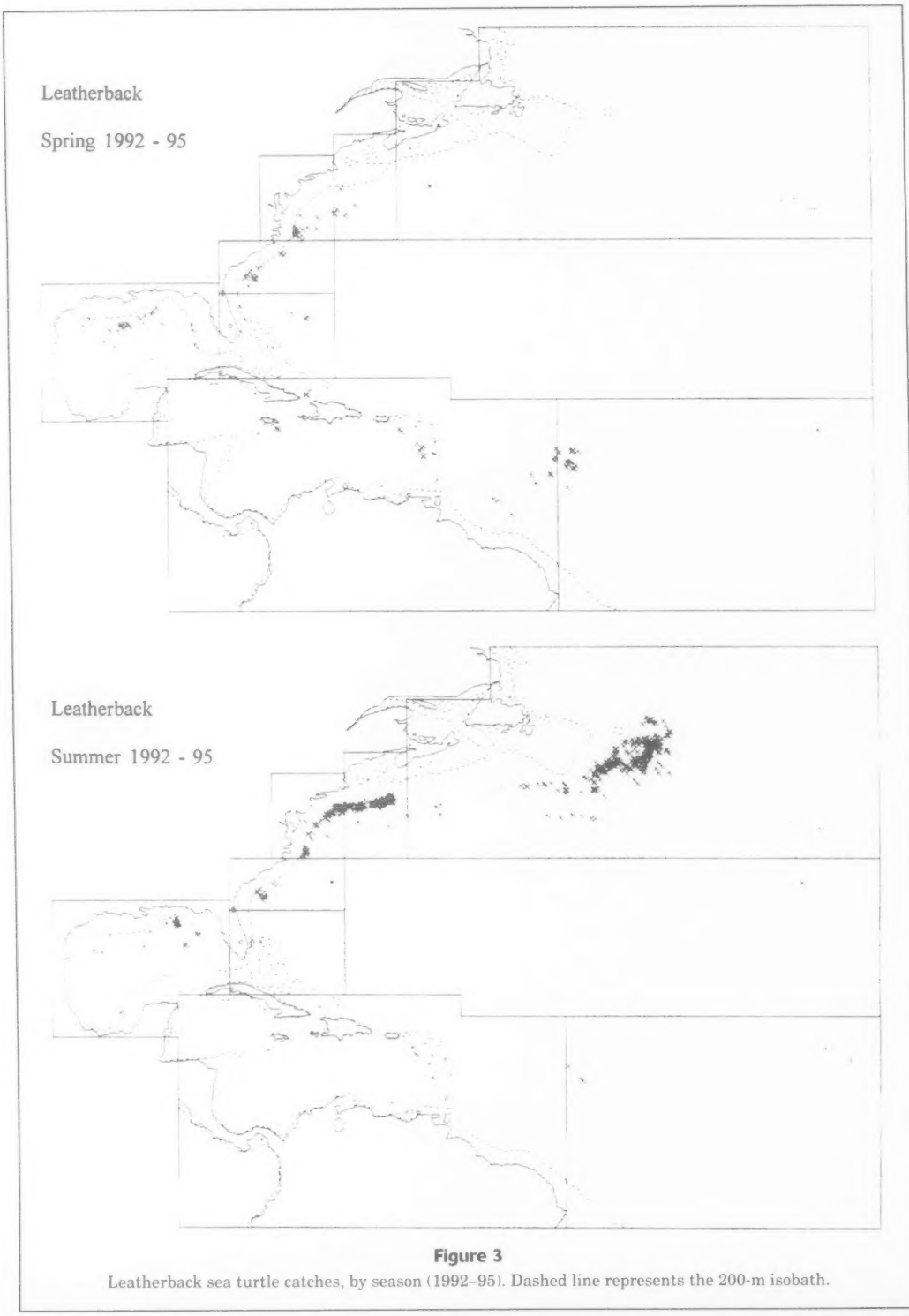


Figure 3

Leatherback sea turtle catches, by season (1992–95). Dashed line represents the 200-m isobath.

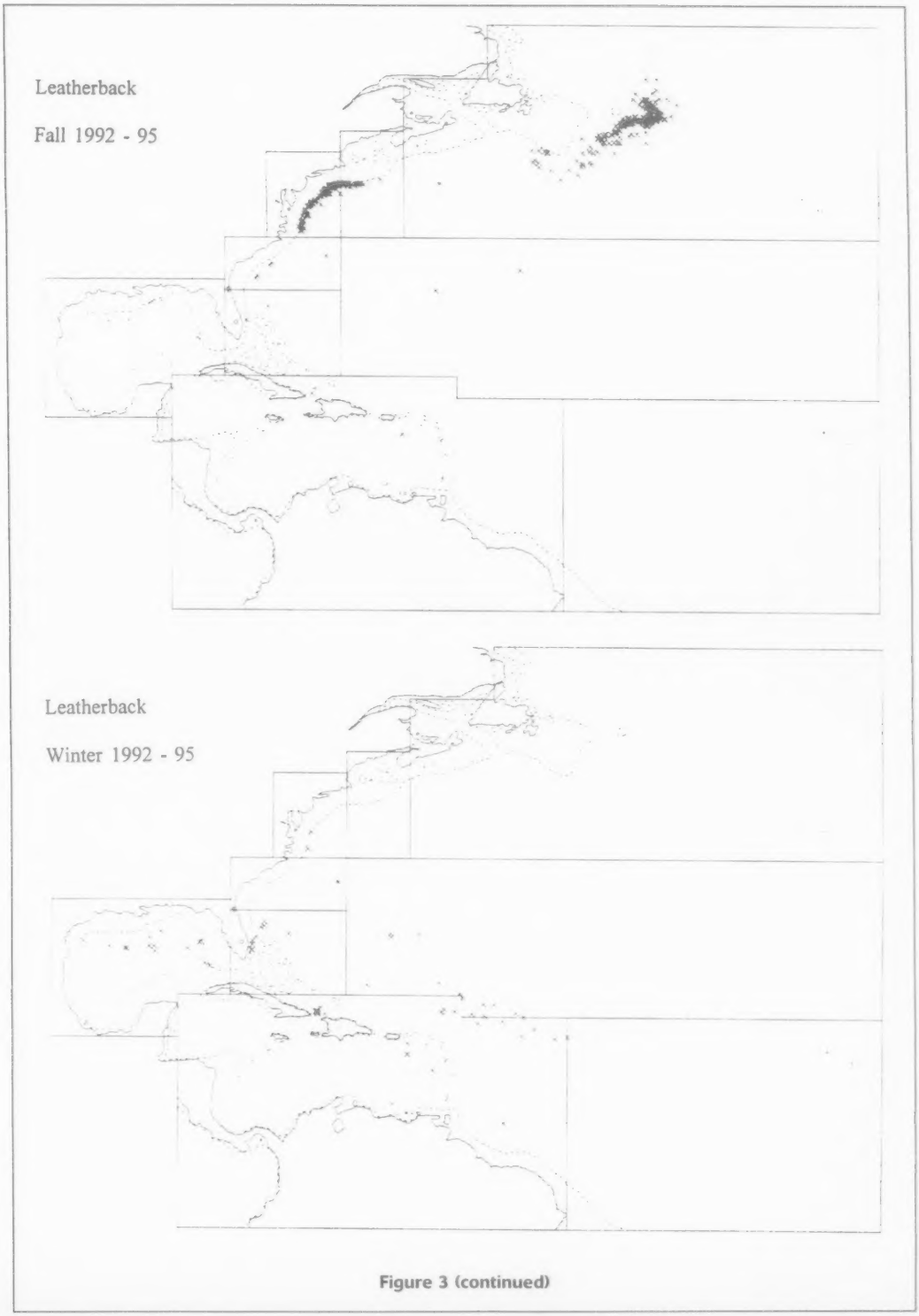


Figure 3 (continued)

Table 1

Leatherback (Lb) and loggerhead (Lh) turtle captures by the U.S. pelagic longline fleet, by NMFS fishing area, by month, for 1992–95.

	Area 1		Area 2		Area 3		Area 4		Area 5		Area 6		Area 7		Area 8		Area 9		All areas combined	
Month	Lb	Lh	Lb	Lh	Lb	Lh	Lb	Lh	Lb	Lh	Lb	Lh	Lb	Lh	Lb	Lh	Lb	Lh	Lb	Lh
01	16	12	4	6	4	2	0	0	1	4	0	0	0	0	0	0	5	4	30	28
02	17	7	12	1	2	3	0	0	0	7	0	0	0	0	0	0	2	3	33	21
03	13	24	8	4	6	2	3	1	6	7	0	0	0	0	4	2	0	1	40	41
04	4	4	7	3	2	1	3	2	1	3	2	1	0	0	1	1	0	0	20	15
05	5	1	1	4	1	1	7	4	13	3	5	3	0	0	11	1	0	0	53	17
06	1	1	3	9	2	1	6	3	22	24	35	49	40	39	3	0	1	0	113	126
07	2	0	10	5	0	0	3	3	19	10	48	62	170	233	0	0	0	0	252	313
08	3	0	10	7	1	0	2	2	32	24	48	14	152	212	0	0	0	0	248	259
09	0	1	0	1	1	1	4	2	76	11	30	4	167	310	0	0	0	0	278	330
10	1	1	2	5	1	0	0	3	84	8	12	6	56	123	0	0	0	0	156	146
11	3	1	3	2	0	1	2	0	7	5	0	4	8	19	0	0	2	0	25	32
12	4	4	3	1	3	1	0	0	1	2	0	0	0	0	0	0	5	1	16	9
Total	69	56	73	48	23	13	30	20	252	108	180	143	593	936	19	4	15	9	1264	1337

in the northeast distant (area 7). The overall CPUE for leatherback sea turtles caught by longline vessels using chemical light sticks was higher than the CPUE with vessels not using light sticks (Table 3), suggesting that the chemical light sticks might simulate bioluminescent gelatinous prey and attract leatherback sea turtles to the branchlines. Fortunately, these turtles tend to become entangled in the branchlines rather than consume baited hooks.

Leatherback sea turtles inhabit coastal and offshore pelagic waters in the North Atlantic Ocean (Pritchard, 1971). Morreale et al. (1994) speculated that they migrated along specific bathymetric contours outside the 200-m isobath, and Lutcavage (1996) proposed that they seek high concentrations of gelatinous prey along the oceanic fronts and meanders of the Gulf Stream. Shoop and Kenney (1992) reported that most were scattered along the continental shelf, except off Rhode Island in 1978, when a number of individuals were observed in association with a large concentration of *Cyanea*. Pelagic longline data, however, suggest that large numbers of leatherback sea turtles apparently also inhabit deep waters extending over the edge of the continental shelf outside the 200-m isobath from Cape Hatteras, North Carolina, to Georges Bank and the Grand Banks in the summer and fall months.

Loggerhead sea turtles

A total of 1337 loggerhead sea turtle captures were recorded in NMFS pelagic logbooks, 1992–95 (Table 1).

Table 2

Leatherback (Lb) and loggerhead (Lh) turtle captures by the U.S. pelagic longline fleet, by NMFS fishing area, by year.

	1992		1993		1994		1995	
Area	Lb	Lh	Lb	Lh	Lb	Lh	Lb	Lh
1	19	12	17	6	8	11	25	27
2	20	9	25	8	12	6	16	25
3	3	2	6	4	11	3	3	4
4	10	2	3	6	7	5	10	7
5	147	30	68	13	29	32	18	33
6	81	26	54	51	19	19	26	47
7	84	59	67	33	105	278	337	566
8	0	0	0	1	3	0	16	3
9	5	0	5	5	4	2	1	2
Total	369	140	245	127	198	356	452	714

Total numbers of individual turtles caught are unknown because observer data indicate that some turtles may have been captured more than once. Year-round loggerhead sea turtle captures averaged 334 individuals per year (range: 127–714); June through November was the most productive period with 1174 (87.8%) captures. The mid-Atlantic Bight, northeast coast, and northeast distant waters (areas 5–7) were the most productive with a combined total of 1187 (88.7%) loggerhead sea turtle captures. Of these, the northeast distant area (7) accounted for 936 (70.0%) of the captures. Like leatherback sea turtles, logger-

Table 3

Leatherback (Lb) and loggerhead (Lh) turtle incidental CPUE from 1992–95 pelagic logbooks, by area, with (Y) and without (N) chemical light sticks. CPUE is turtle captures per 1000 hooks fished.

Area	Lights	Hooks	Lb Captures	Lh Captures	Lb CPUE	Lh CPUE
1	Y	1,036,600	66	54	0.0637	0.0521
1	N	101,716	3	2	0.0295	0.0197
2	Y	2,580,340	38	37	0.0147	0.0143
2	N	3,132,180	35	11	0.0112	0.0035
3	Y	1,389,240	23	13	0.0166	0.0094
3	N	45,773	0	0	0.0000	0.0000
4	Y	937,620	30	19	0.0320	0.0203
4	N	88,089	0	0	0.0000	0.0114
5	Y	1,523,970	154	53	0.1011	0.348
5	N	2,052,910	108	55	0.0526	0.0268
6	Y	1,356,540	132	83	0.0973	0.0612
6	N	835,484	48	60	0.0575	0.0718
7	Y	2,086,660	591	932	0.2832	0.4466
7	N	55,214	2	4	0.0362	0.0724
8	Y	51,593	18	4	0.3489	0.0774
8	N	1,285	1	0	0.7782	0.0000
9	Y	497,265	15	9	0.0302	0.0181
9	N	25,696	0	0	0.0000	0.0000
1–9	Y	11,459,800	1067	1204	0.0931	0.1051
1–9	N	6,338,350	197	133	0.0311	0.0210

head sea turtles were sporadically captured throughout the entire fishing area in the winter and spring and became abundant during the summer and fall in fishing areas 5–7 (Fig. 4). September was the most productive month with a combined total of 330 (24.7%) loggerhead sea turtle catches. Reported catches varied annually (Table 2). The mean curved carapace length (nuchal notch to tip of marginal) and weights of these captured sea turtles from the north east distant area (7) were 55.9 cm (SD=6.5 cm, n=98) and 22.1 kg (SD=11.1 kg, n=72). These turtles were smaller than coastal loggerheads from the northeastern United States (Lutcavage and Musick, 1985).

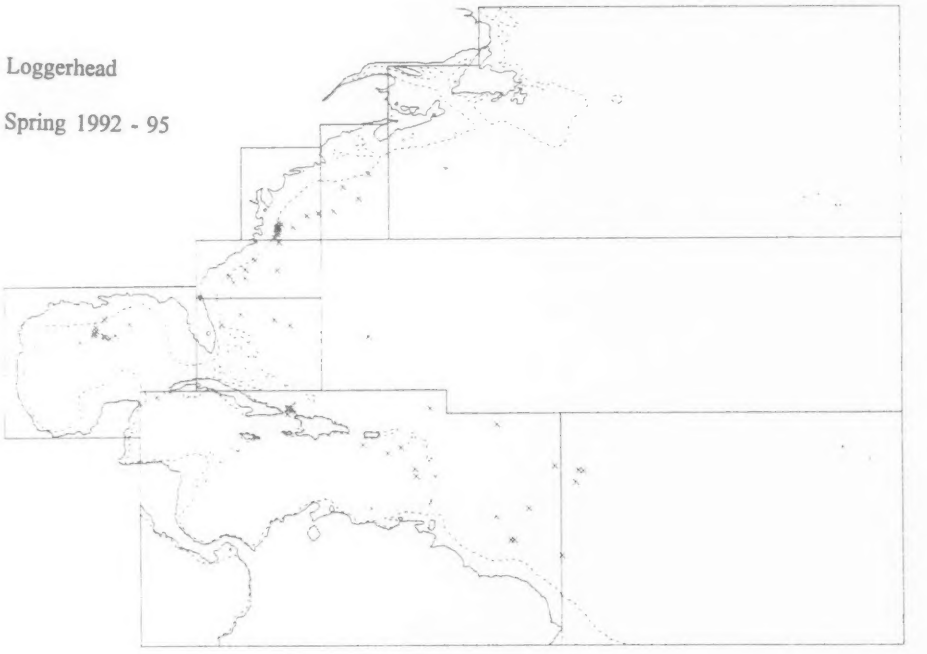
CPUE values indicated that loggerhead capture rates varied between areas (Table 3) and were highest for the northeast distant area (7). CPUE analysis indicated that the overall loggerhead sea turtle capture rates with light sticks were higher than the CPUE without light sticks (Table 3). Unlike leatherback sea turtles, loggerhead sea turtles readily consumed baited hooks. The fate of such hooked turtles is unknown, but they have been observed trailing multiple gangions; therefore some turtles previously hooked have remained actively feeding in the area.

Pelagic longline data indicate that loggerhead turtle distribution extends from coastal waters to the edge of the continental shelf from Cape Hatteras, North Carolina, to Georges Bank and the Grand Banks in the summer and fall months and also extends into deep waters off the shelf. These turtles are apparently able to move out of critically cold winter slope water to more hospitable southern waters. NMFS tagging data revealed that turtles hooked on their flippers were tagged in the spring in areas 6 and 7 and recovered in warmer winter waters in areas 4 and 2, respectively (NMFS[3]).

Conclusions

It is not surprising that pelagic longline fisheries incidentally catch turtles because fishing effort is concentrated either near the 200-m isobath or near interactions between major current systems. In these areas a variety of potential prey species (various nektonic organisms associated with *Sargassum,* as well as cephalopods, coelenterates, and schooling fish) concentrate and consequently attract tunas, swordfish, and sharks (Laurs et al., 1984; Maul et al., 1984; Kurowicki, 1987; Fiedler and Bernard, 1987; Podesta et al., 1993; Lutcavage, 1996). Aerial survey data off the eastern United States (Shoop and Kenney, 1992) and pelagic longline data presented here indicate that

[3] NMFS Cooperative Marine Turtle Tagging Program, Miami Laboratory, 75 Virginia Beach Drive, Miami, FL 33149.



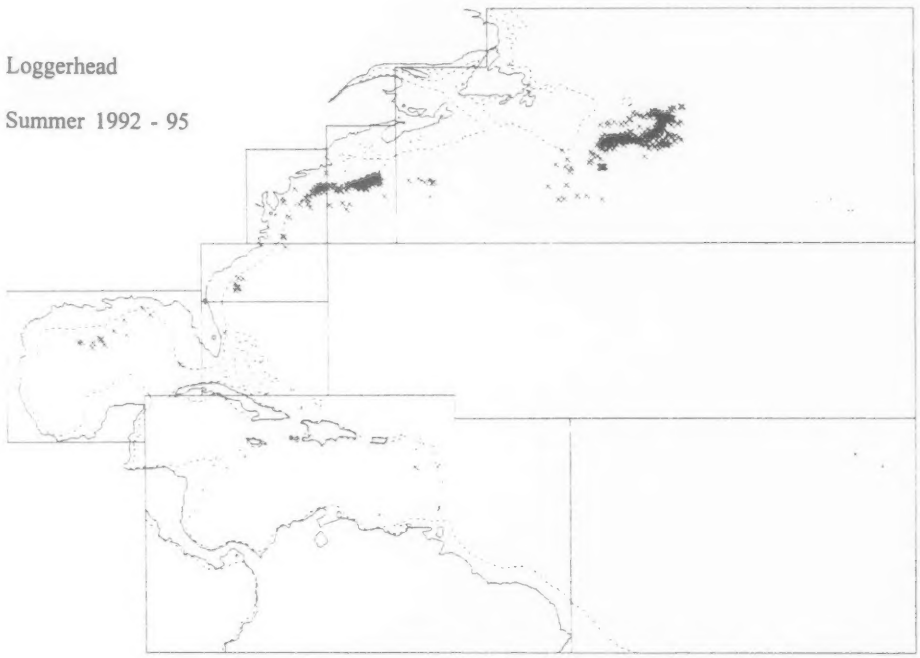


Figure 4

Loggerhead sea turtle catches, by season (1992–95). Dashed line represents the 200-m isobath.

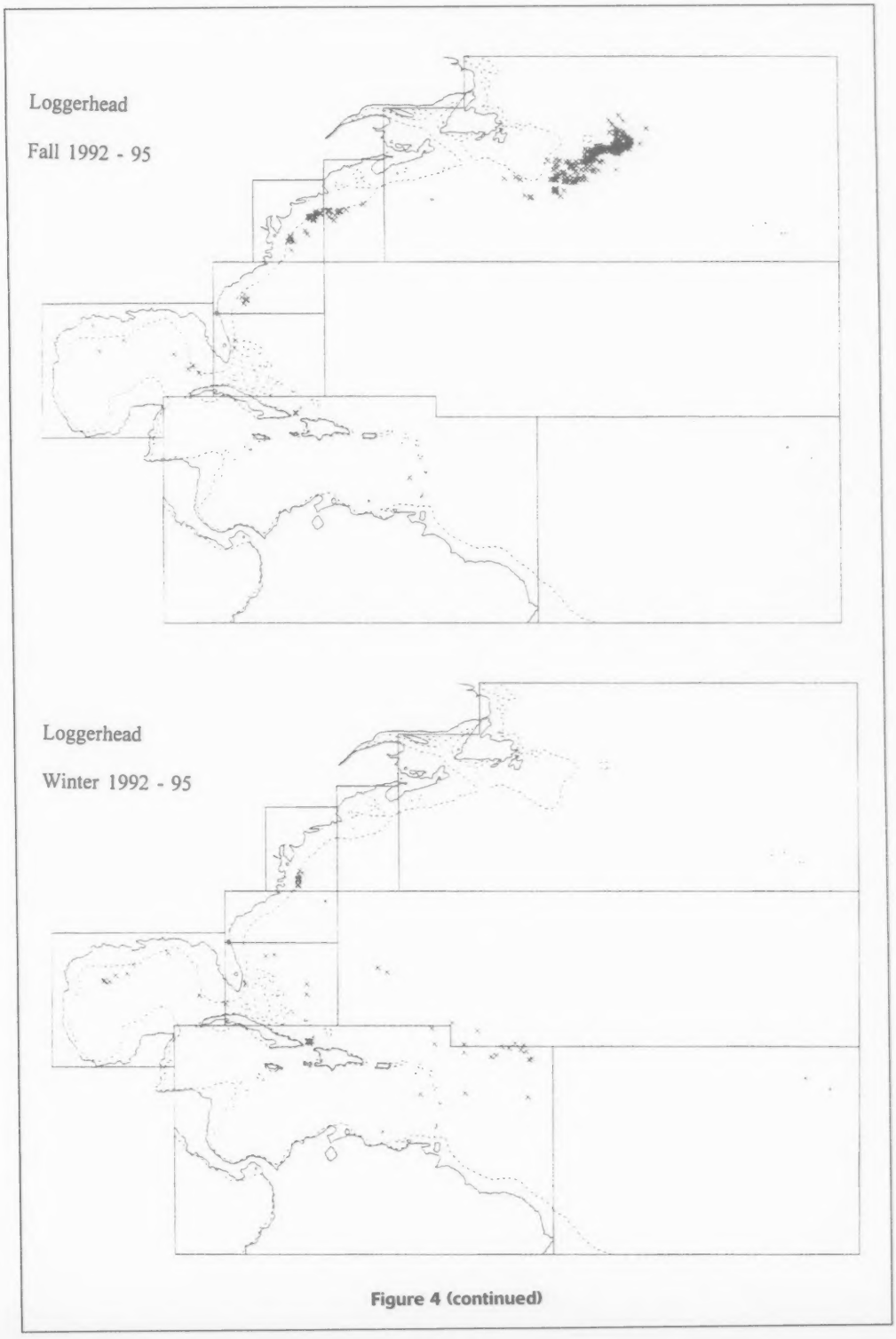


Figure 4 (continued)

leatherback and loggerhead sea turtles use the entire continental shelf, as well as the thermally dynamic waters off the continental edge.

The northeast distant fishing area (7) is particularly productive. The circulation and thermodynamics of fishing area 7 are very complex and provide a unique pelagic habitat. The Gulf Stream begins to meander northeastward off Cape Hatteras, and the western edge of the Gulf Stream eventually passes south of the Grand Banks as it turns eastward toward Europe. The thermodynamics of north Atlantic circulatory process near the Grand Banks is complicated (Schmitz and McCartney, 1993), and it is this interaction of cold slope water and warm Gulf Stream water that is productive for large pelagic fish and sea turtles. Moreover, the Gulf Stream spins off warm-core rings on the cooler northeastern slope water (Auer, 1987), where pelagic longline fishing is heaviest. These warm-core rings have been well studied, resulting in a plethora of published literature (Wiebe and McDougall, 1986). Unfortunately, these biological studies have concentrated on planktonic productivity and mesopelagic fishes rather than on larger pelagic apex predators; however, these rings affect the distribution and abundance of large pelagic fish, marine mammals, and sea turtles.

Fishery managers and sea turtle researchers need to develop conservation strategies that mitigate sea turtle and longline interactions. The high numbers of potentially lethal loggerhead sea turtle captures in the northeast distant area (7) during the summer and fall swordfish fishery particularly need to be addressed by fishery managers.

Acknowledgments

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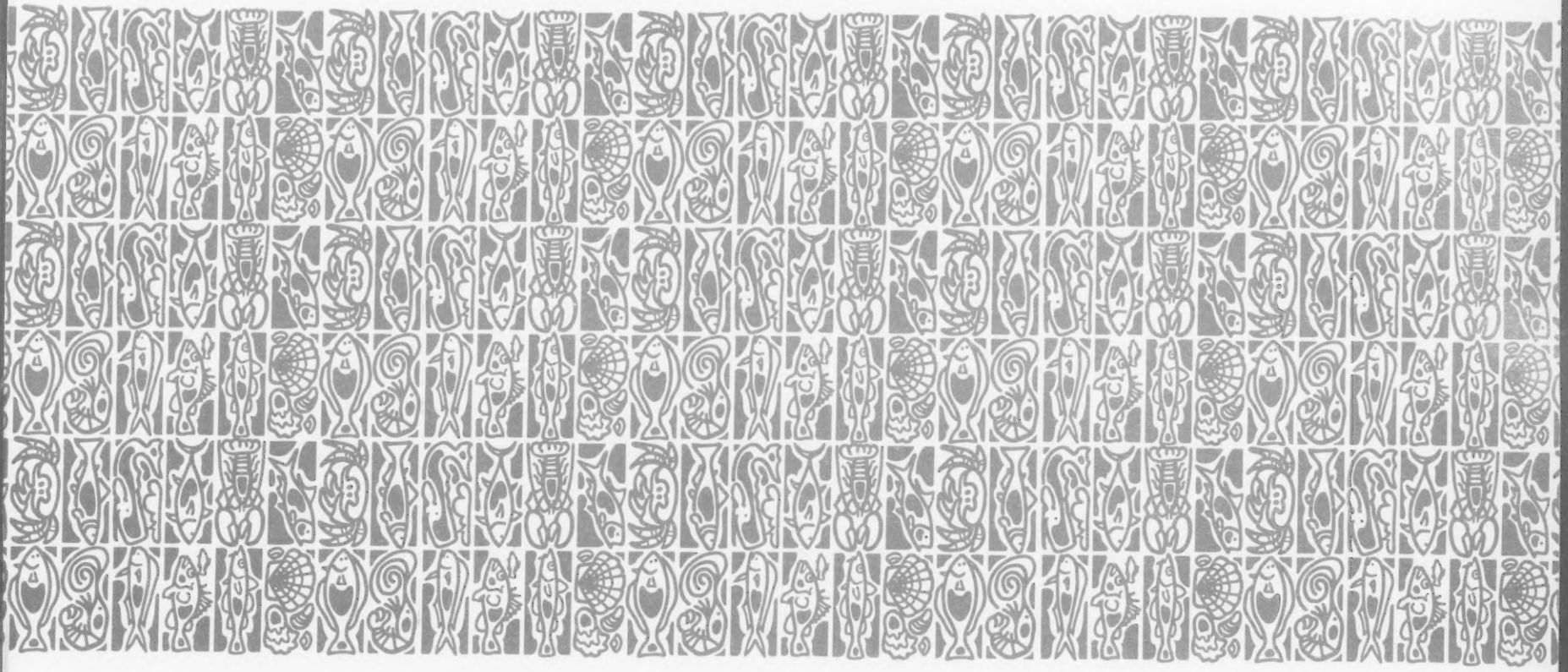
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